Perception across saccadic eye movements: On the interrelationship between pre- and postsaccadic information

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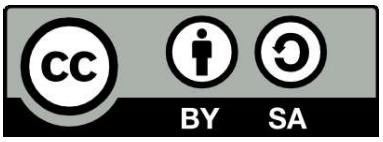

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1 Summary

This dissertation is devoted to the question of how the healthy human brain generates visual experience of its environment, in its homogenous and coherent nature, given the stream of heterogeneous and incoherent information available to the visual system. Heterogeneity refers to the varying spatial resolution of visual information processing across the visual field (fovea to periphery) and incoherence to disruptions of visual information by fast jerk-like eye movements called saccades. Both of these aspects and their implications are described in the Introduction. Individual approaches and outcomes of four studies, each contributing to the understanding of the issue of visual stability stated above, are outlined subsequently.

To gain understanding on whether and how information from before and after a disruptive saccade is integrated into perception, the first study (Study I) investigated whether perception of a stimulus observed across a saccade can be predicted by a statistically optimal integration of pre- and postsaccadic signals. Results revealed that perceptual performance was close to predictions for optimal transsaccadic integration. Integration even seemed to occur when the presented stimulus changed some visual properties during the saccade.

As the result of the first study implied that integration of pre- and postsaccadic information is a phenomenon that is robust against visual discrepancies, the question emerged as to what would lead to transsaccadic segregation i.e., a percept of discrepancy between the pre- and postsaccadic information. Driven by the idea that the ability to integrate or segregate information develops over the lifespan, the second study (Study II) aimed to investigate transsaccadic segregation in children compared to young adults. The study showed that children detect stimulus displacements across a saccade less precisely than adults, indicating less transsaccadic segregation at childhood. However, children's segregation abilities showed a stronger improvement due to the implementation of a perceptual aid (postsaccadic blank) compared to adults. In addition, children made less accurate and less precise saccades than adults but were also faster to correct their saccade landing errors. These results suggest that saccadic uncertainty (expectations about self-induced position errors) play a role in transsaccadic perception.

To further determine the principles guiding transsaccadic segregation, the third study (Study III) investigated perception of intrasaccadic shape changes (circularity increase or decrease), and its relationship with shape appearance across the visual field. Results revealed that shape changes where we increased circularity across saccades were more likely to be perceived by participants (than circularity-decrease changes). In addition,

shape appeared more circular before a saccade in the peripheral visual field compared to after a saccade in the fovea. These results suggest the existence of a predisposition to detect shape changes opposite (circularity increase) to the typical transsaccadic experience (circularity decrease). This gives further support to the assumption that expectations regarding transsaccadic contingencies play a key role in the ability to detect intrasaccadic changes.

The fourth study (Study IV) turned towards the issue of how presaccadic visual stimulation affects postsaccadic perception and investigated the effect of short-term luminance adaptation before a saccade on contrast perception after the saccade. Results revealed that postsaccadic perception can be altered by presaccadic adaptation during very short durations corresponding to natural fixation durations.

To conclude, transsaccadic perception is determined by the integration or segregation of pre- and postsaccadic information. Study I revealed that transsaccadic integration can occur despite large intrasaccadic stimulus changes. Studies II and III suggest that transsaccadic segregation depends on typical transsaccadic experience. Study IV showed that transsaccadic perception is likely to be affected by basic aspects of visual information processing such as adaptation. Taken together, this dissertation suggests that the visual system has developed statistically optimal and predictive mechanisms for heterogeneous and incoherent information to result in a coherent and adaptable perception of the environment.

2 Introduction

Any living organism must process information available from its environment and it must process the appropriate amount and the right kind of information necessary to survive and thrive. Primates, including humans, developed the following way to process visual information: their visual sensors i.e., their retinae contain a circular arrangement of millions of photoreceptors that have their highest density at a central pit: the fovea centralis (Oesterberg, 1935; Curcio et al., 1990; for a review see Hendrickson, 2005). The information from the area of the environment that reaches the retina is further propagated through early and later visual processing stages in the brain. The processed information results to be perceived in a spatial array of visual sensations that is referred to as the visual field (for a review see Smythies, 1996). Congruent with the anatomy of the retina and with the high proportion of cortical tissue dedicated to processing information coming from the fovea centralis (e.g., Dow et al., 1981; Azzopardi & Cowey, 1993; Dumoulin & Wandell, 2008), the centre of the visual field provides maximal visual acuity (Aubert & Foerster, 1857; Wertheim, 1894). The centre of the visual field will further be referred to as the fovea. The large peripheral area surrounding the fovea comprises a less detailed and more spatially distorted representation of the environment (for reviews, see Strasburger et al., 2011; Rosenholtz, 2016). For example, perceptual localisation of objects and features is more variable in the periphery of the visual field meaning that the exact location or spatial arrangement of something is harder to estimate when not directly viewed in the fovea (Rentschler & Treutwein, 1985). Another example is that objects in clutter are more difficult to correctly identify in the periphery; a phenomenon called visual crowding (Korte, 1923; Bouma, 1970).

Given that the peripheral visual field encompasses a large area of the environment but also implies obvious disadvantages for object recognition, humans shift their gaze such that relevant objects will land in the fovea (for a review see Schütz et al., 2011). These gaze shifts are usually achieved by rapid jerk-like eye movements called saccades. This rapid eyeball rotation has several dramatic consequences for vision, aside from the changes in appearance of object information with gaze shifts. One consequence is that during the eye motion, visual input to the retina changes too quickly to be resolved clearly, leading to a visual smear. This may be similar to what one perceives when fixating on a point near the railroad track out of a window on a train moving at high speed. Here, one might notice that fine visual detail becomes invisible (grey-out of high spatial frequencies), but that lower spatial frequencies such as the part of the rail parallel to the train or some separated trees remain visible and become rather salient. That high spatial frequencies grey out and

low spatial frequencies remain visible is also true when visual smear due to saccade-like motion speeds is perceived during fixation (Burr & Ross, 1982). However, one usually does *not* perceive the smear caused by their own saccades, a phenomenon referred to as saccadic omission (Campbell & Wurtz, 1978). One reason for this lack of visual experience during saccades seems to be masking by the close-by high contrast information (the pre- or postsaccadic information, Matin et al., 1972; Campbell & Wurtz, 1978; Duyck et al., 2016; Idrees et al., 2020) and it has been linked to a decrease in visual sensitivity during and even shortly before saccades (Volkmann, 1962; Volkmann et al., 1968); a phenomenon that has been coined saccadic suppression (Zuber & Stark, 1966) or more specifically, saccadic suppression of contrast sensitivity (SSCS, for reviews, see Ross et al., 2001; Wurtz, 2008; Higgins & Rayner, 2014).

Even though visual input around the time of saccades i.e., perisaccadic information is omitted or suppressed, this does not cause a gap in perception. In fact, visual perception appears to be continuous; this intriguing phenomenon has been termed visual stability (for reviews, see Melcher & Colby, 2008; Mathôt & Theeuwes, 2011; Melcher, 2011). One leading research question in the field of visual stability is: how do the supposedly disconnected chunks of pre- and postsaccadic information be reconciled and lead to continuous perception?

The problem of correspondence between disconnected sensory information has formally been addressed by applying causal-inference models (for a review see Shams & Beierholm, 2010). Causal inference refers to the evaluation of the most likely cause behind the occurrence of two or multiple independent signals. Depending on the correlation between signals and prior expectations, they could be assigned to be due to a common cause or each could be assigned to a different cause. A model based on causal inference has also been successfully applied to transsaccadic perception of object location (Atsma et al., 2016). This model assumes that pre- and postsaccadic location information could either have a common cause or no common cause. The assignment of a common cause results in *integration* of the two (a single percept) while no common cause keeps the two signals *segregated* (distinct pre- and postsaccadic percepts). Each of these causal structures (i.e., integration vs. segregation) is then weighted by their respective probability that is estimated from the discrepancy between pre- and postsaccadic location information and the precision of this error.

The concept behind the model by Atsma et al. (2016) of transsaccadic perception represents the theoretical basis of this dissertation. It has two important implications: 1) integration and segregation are the two opposing outcomes of the same mechanism such that more integration automatically leads to less segregation and vice versa; 2) optimal integration (i.e., full integration) of pre- and postsaccadic information requires low discrepancy between pre- and postsaccadic information since higher discrepancy should increase the weight for segregation. Besides the findings of the four studies of this thesis, both of these implications will be evaluated in the Discussion. In the following sections of

the Introduction, the concepts behind, and evidence for transsaccadic integration (section 2.1) and transsaccadic segregation (section 2.2) will be explained. Further, two additional important aspects of transsaccadic perception will be introduced: the ability of the visual system to predict postsaccadic information (section 2.3), and how the neuronal property of adaptation contributes to transsaccadic perception (section 2.4).

2.1 Integration of transsaccadic information

Early ideas on how pre- and postsaccadic information could be reconciled were based on the discovery that a presaccadic image would still be visible after the saccade even if the stimulus was removed from the experimental screen (W. Wolf et al., 1980). Highly detailed, spatially accurate image compositions seemed to result: for example, an arrangement of dots shown before a saccade would fuse with another arrangement of dots shown only after the saccade, which was then perceived as one arrangement containing all these dots (in a 5 x 5 dot matrix; Jonides et al., 1982). However, this conclusion was quickly refuted as it was found that the kind of monitors the researchers used (CRT monitors) caused the persistence of the visual information on screen rather than the persistence of visual information within the brain (Jonides et al., 1983; O'Regan & Lévy-Schoen, 1983). This was accompanied by a series of studies (using appropriate monitors) that could not find evidence for so called transsaccadic fusion (Irwin et al., 1983; Rayner & Pollatsek, 1983; Bridgeman & Mayer, 1983). Nevertheless, a more recent study by Paeye et al. (2017) found evidence for transsaccadic fusion when they optimised the stimulus conditions to be able to measure the effects of fusion (low postsaccadic stimulus contrast and no requirement for spatially accurate alignment of the image information).

While transsaccadic fusion suggests a low-level image-based integration of pre- and postsaccadic information, other studies suggested a mid-level or higher-level process where pre-processed presaccadic information is encoded into transsaccadic memory to then be integrated with the incoming postsaccadic information (e.g., Irwin et al., 1990; Demeyer et al., 2009; for a recent review see Aagten-Murphy & Bays, 2019). This interpretation was driven by findings suggesting that pre- and postsaccadic information influenced each other. For instance, recognition of a postsaccadic stimulus was found to be faster and more accurate when the presaccadic stimulus was identical or of the same category (e.g., Pollatsek et al., 1984; Henderson et al., 1987); postsaccadic colour perception was found to be biased in the direction of the presaccadically presented colour (Wittenberg et al., 2008); and such a bias was even found to be weighted optimally (Oostwoud Wijdenes et al., 2015). This means that the pre- and postsaccadic colour information influenced the participants' perceptual reports in a manner that follows one of the principles of Maximum-likelihood estimation (MLE, explained below).

MLE represents a statistically optimal manner for the integration of two or more cues (for a review see Ernst & Bülthoff, 2004). A cue is considered a signal or the information

processed from that signal e.g., some sensation of an object. Separate cues are assumed to be independent such that each signal will be subject to independent, Gaussian noise. When two or more cues are integrated, the mean of the integrated signal equals the weighted sum of the cues' means, while a cue has more weight the more reliable it is. Reliability refers to statistical reliability of a cue and is typically defined to be inversely related to the variance over all estimates based on that cue. For instance, colour estimates collected across several trials may be more variable when the stimulus was perceived in the periphery compared to the fovea, which would mean that the peripheral cue or information was less reliable. If transsaccadic integration of presaccadic peripheral and postsaccadic foveal information is optimal, the transsaccadic percept should be less influenced by the less reliable presaccadic information (Oostwoud Wijdenes et al., 2015). However, optimal weighting is not sufficient evidence to conclude that transsaccadic information was indeed integrated optimally. Such an observation could also be caused by "cue switching". Cue switching describes the possibility that participants could either report the presaccadic or the postsaccadic percept only and that they alternate between these two options across trials (without ever experiencing an integrated percept). The mean taken over all trials would hence also reflect a percept averaged across more or less reliable pre- and postsaccadic estimates. To rule out this possibility, one can test another prediction made by MLE: the reliability of the integrated signal should be larger than the maximum reliability of the single cues. Specifically, it should equal the summed single-cue reliabilities. This prediction has been successfully tested for multisensory perception. For instance, given visual and haptic information on the size (Ernst & Banks, 2002) or the shape of an object (Helbig & Ernst, 2007), the integrated visuo-haptic percept was even more reliable than the most reliable single percept alone (e.g., undisturbed visual information).

The first works showing that both MLE predictions (mean averaging and reliability enhancement) can apply to transsaccadic perception came from Ganmor et al. (2015) and Wolf and Schütz (2015). Both teams showed a stimulus containing orientation information (gratings tilted clockwise or counter clockwise) either exclusively before a saccade or after a saccade and they manipulated the reliability of those individual pre- or postsaccadic cues by varying the stimulus contrast. When both pre- and postsaccadic orientation information was provided, the mean and the reliability of the estimates in this integration condition could be closely predicted by optimal (MLE) cue integration. An interim conclusion may be that pre- and postsaccadic information is reconciled by statistically optimal transsaccadic integration by means of transsaccadic memory (storage of abstracted presaccadic information across a saccade). However, Paeye et al. (2017) argued that the reliability improvement found by Ganmor et al. (2015) and Wolf and Schütz (2015) could also be due to a persisting image of the presaccadic information that was adding to the perception of the postsaccadic stimulus i.e., due to transsaccadic fusion. This open question will be addressed in Study I of this dissertation.

2.2 Segregation of transsaccadic information

As outlined previously, visual stability is not a trivial outcome of visual information processing when one considers the abrupt changes in information processing that saccadic eye movements cause. The visual system seems to have found elegant mechanisms to overcome those self-induced disruptions and to uncover these, one might investigate how it handles additional, externally caused disruptions. Bridgeman et al. (1975) did this by slightly displacing the saccade target around the time of the saccade. While displacement thresholds are usually very low during fixation i.e., very small displacements can be detected when gaze position is fixed (Legge & Campbell, 1981), Bridgeman et al. (1975) found detection thresholds for intrasaccadic displacements to be substantially higher, increasing with saccade amplitude (the distance gaze travels over a saccade). In addition, the ability to detect displacements seems to be related to the decrease in contrast sensitivity around the time of saccades, such that a motion transient that might be used to inform displacement perception cannot be perceived. Therefore, this phenomenon is referred to as saccadic suppression of image displacement or saccadic suppression of displacement (SSD).

Models applied to explain SSD suggest that the visual system needs to compare the location information it gets from before and after the saccade and decide whether to *segregate* this information in order to detect a target displacement, or to integrate the pre- and postsaccadic information but potentially miss a displacement (Atsma et al., 2016). Since the localisation of targets in the periphery is error prone (localisation uncertainty) and so is the execution of the saccade (motor noise) it has been suggested that the visual system needs to make the decision by taking into account this saccadic uncertainty (Niemeier et al., 2003; Atsma et al., 2016). For example, a model applied by Niemeier et al. (2003) was based on a so-called stability assumption (MacKay, 1972), which is a prior assumption that the external world is likely to remain unchanged during the time of a saccade. This prior probability should lead to a displacement not being perceived, if saccadic uncertainty was high. As saccade landing variability, and hence saccadic uncertainty, is lower on the axis orthogonal to a saccade, the model could also successfully predict lower detection thresholds for orthogonal target displacements (Niemeier et al., 2003, 2007).

Twenty-one years after the discovery of SSD, the rather surprising discovery was made that participants were able to regain their ability to detect displacements when the saccade target was not presented upon saccade landing but after a brief postsaccadic blank period (50 to 300 ms; Deubel et al., 1996). This blanking effect could again be explained by the use of a stability assumption: a postsaccadic target disappearance represents unmistakeable evidence against environmental stability and therefore, the influence of this prior is nullified (Niemeier et al., 2003). Alternative theoretical accounts that were proposed to explain the blanking effect emphasise the extra amount of input-free time during the blank period, which could enable either a sufficient read-out of the presaccadic target information, or could provide sufficient time to process upcoming postsaccadic information

outside the time window of suppression of contrast sensitivity (e.g., Zimmermann et al., 2013; Ziesche et al., 2017). However, these accounts cannot explain other characteristics of transsaccadic segregation for example, lower detection thresholds for orthogonal displacements (Niemeier et al., 2003, 2007). Nevertheless, the reason why target blanking helps to segregate pre- and postsaccadic information is under debate (Born, 2019). To single out a comprehensive theory for transsaccadic segregation including the effect of blanking, it is of unquestionable importance to further characterise transsaccadic segregation performance. Two of the studies in this dissertation (Study II and Study III) have been dedicated to this objective.

2.3 Prediction of postsaccadic information

Stimulus location certainly is the most studied feature in intrasaccadic-change detection research (more than 25 studies, e.g., W. Li & Matin, 1990; Currie et al., 2000; Gysen et al., 2002; Niemeier et al., 2007; Collins et al., 2009; Ostendorf et al., 2010; Tas et al., 2012; Wexler & Collins, 2014). Considering that the visual-feature space is large, the literature regarding transsaccadic segregation of other features like: object contour (Henderson, 1997; Demeyer et al., 2010b), form (Deubel et al., 2002; Grzeczkowski, van Leeuwen et al., 2020), orientation (Henderson & Hollingworth, 1999; De Graef & Verfaillie, 2002; Grzeczkowski, Deubel et al., 2020), luminance (Henderson et al., 2008), and spatial frequency (Weiß et al., 2015) is comparably sparse. For a comprehensive understanding of transsaccadic segregation, however, it is vital to investigate all feature changes, as any feature information should be processed differently across the visual field. Those visual-field differences in feature appearance are interesting because a saccade should cause systematic appearance changes of stationary objects (O'Regan & Noë, 2001). For example, spatial frequency appears to be higher in the periphery compared to when it is viewed in the fovea (Davis et al., 1987). The typical experience that should follow from making a saccade towards an object of a certain spatial frequency (e.g., a grating) is that its spatial frequency should decrease in the saccade direction (from presaccadic peripheral view to postsaccadic foveal view). Such transsaccadic contingencies should be the laws that govern transsaccadic experience and the visual system might use these laws to predict postsaccadic information following the presaccadic information (Ehinger et al., 2015).

One way to test whether the visual system learns from transsaccadic contingencies and whether this learning influences perception is the following: in an exposure- or acquisition phase participants get repeatedly confronted with a certain artificially manipulated transsaccadic contingency. In a subsequent test phase, participants judge the appearance of a (presaccadic) peripheral stimulus and this judgement should be biased towards the associated postsaccadic appearance if the precedent learning was effective (Cox et al., 2005). For example, Herwig and Schneider (2014) changed the spatial frequency of a grating stimulus across a saccade in an acquisition phase. One group of participants was exposed

to intrasaccadic changes that decreased the spatial frequency towards postsaccadic vision and the other group experienced spatial-frequency increases. In the test phase, both groups showed a bias indicating that the presaccadic peripheral stimulus (that was associated with the change) appeared to be more alike to the associated postsaccadic stimulus. Such effects on presaccadic peripheral appearance have been found for several visual features such as shape (Cox et al., 2005; Herwig et al., 2015; Paeye et al., 2018; Köller et al., 2020), object size (Valsecchi & Gegenfurtner, 2016), and even higher-level features such as object category and gender of faces (Osterbrink & Herwig, 2021).

Based on the findings that peripheral appearance was biased by how objects appeared when perceived with foveal vision, it has been suggested that transsaccadic predictions, that is, a prediction of the postsaccadic information based on transsaccadic experience/expectations triggered by the presaccadic information, serve to"calibrate" presaccadic peripheral perception to achieve the impression of uniformity throughout the visual field (Valsecchi & Gegenfurtner, 2016). Another and perhaps more important function of transsaccadic predictions may be the realisation of rapid and accurate postsaccadic perception (Fabius et al., 2016). Edwards et al. (2017) showed that this may be achieved by a predictive visual signal generated in higher-level areas sent to the primary visual cortex (V1). Crucially, this predictive signal was found to be sent to neural populations in V1 that process the upcoming postsaccadic information (foveal neurons). Such transsaccadic predictions attenuated activity in this area when the postsaccadic information matched the prediction and increased activity when the prediction was not matched. This is in line with the concept of a prediction error (degree of mismatch between prediction and sensory input) postulated in the predictive coding framework (Rao & Ballard, 1999; Friston, 2009; for a review see de Lange et al., 2018).

A prediction error has been suggested to signal "surprise" and to make the sensation causing it more salient (for a review see den Ouden et al., 2012). Hence, a large prediction error between a transsaccadic prediction and the postsaccadic input should facilitate intrasaccadic change detection. Therefore, it may be the case that transsaccadic predictions serve as a measure to evaluate evidence for or against visual stability i.e., whether something in the environment changed during the saccade or not. This would imply that current transsaccadic input consistent with typical transsaccadic experience (transsaccadic expectations) will be perceived as stable, but that a change would be perceived if it is contrary to transsaccadic expectations. So far, there has been no systematic investigation of natural transsaccadic expectations that have built up over a lifetime, and their impact on transsaccadic perception. Study III of this dissertation aimed to start to fill this gap by investigating the nature of transsaccadic contingencies in regard to the feature shape and their impact on transsaccadic segregation performance.

2.4 Adaptation of presaccadic information

A physiological process mediating transsaccadic perception may be predictive remapping (further referred to as remapping, for a review see Higgins & Rayner, 2014). Remapping is an anticipatory pre-activation of neurons that have their receptive fields in positions that the relevant stimulus will fall into after the saccade (Duhamel et al., 1992; for a recent review see Bisley et al., 2020). It has been found in higher- and mid-level processing areas e.g., in the lateral intraparietal area (Duhamel et al., 1992) and mid-level visual areas (Nakamura & Colby, 2002; Merriam et al., 2007). Remapping is thought to be crucial for converting information coded in retinal coordinates (retinotopic, e.g., Gardner et al., 2008) into a coordinate system that maps where things are in the environment (spatiotopic) and therefore enable visual stability across saccades (for a review see Hall & Colby, 2011).

A way to test effects of predictive remapping in perception is to measure a spatiotopic transfer of adaptation. Adaptation is a ubiquitous neuronal property that is characterised by a reduction of spiking activity and a shift of sensitivity due to prolonged exposure to an unchanging input (for reviews, see Clifford et al., 2007; Kohn, 2007). Any stimulus, for instance a black bar on a white background will reduce the activity of the neurons that respond to it over time and if the stimulation is removed, all non-adapted neurons will exhibit more activity in relation to the adapted neurons. This can produce a negative afterimage (a light bar on a dark background) or an aftereffect, for instance based on the orientation of the bar (e.g., if the adapted bar was tilted to the right of vertical a subsequently perceived vertical bar may appear tilted to the left), called the tilt aftereffect (Gibson & Radner, 1937). An aftereffect is thought to be remapped if adaptation to a presaccadic stimulus in the periphery affects perception of the postsaccadic stimulus in the fovea. For instance, Melcher (2005) showed that adaptation to a tilted grating presented in the periphery induced a tilt aftereffect onto a grating that was viewed after a saccade in the same spatiotopic position as the adapted grating. This remapping of feature-specific information was also found for more higher-level features such as form or gender of faces, while it did not occur for contrast information (see also D. He et al., 2017). Whether feature information or just attention gets remapped is, however, still under debate (e.g., Knapen et al., 2009; Knapen et al., 2010; Cavanagh et al., 2010).

Studies investigating spatiotopic transfer of aftereffects also implemented retinotopic conditions, demonstrating that adaptation before a saccade can strongly affect postsaccadic perception simply in retinotopic coordinates (when the adapted and the test stimulus both project onto the same retinal position, e.g., Knapen et al., 2009; Knapen et al., 2010). This means, that for instance a grating that was observed for at least three seconds at the centre of fixation presaccadically, can influence perception of a saccade target that lands at the centre of fixation after the saccade. While those studies serve as a proof of principle to show behavioural correlates of remapping, the effects reported in conventional transsaccadic adaptation studies are likely irrelevant for natural perception. This is because humans

only fixate over durations of 200 to 300 milliseconds in passive observation (Wilming et al., 2017), which is less than a tenth of the adaptation durations typically used. Although retinotopic luminance afterimages or contrast aftereffects are known to emerge quickly within a few hundred milliseconds of fixation (Foley & Boynton, 1993; Pavan et al., 2012), the strength of an afterimage or aftereffect decreases with shorter adaptation durations (for a review see Kohn, 2007). In addition, changes in visual input counteract adaptation and saccades dramatically change visual information processing (e.g., retinal smear, saccadic suppression; for a recent review see Binda & Morrone, 2018). This opens the question whether afterimages that result from naturally brief adaptation durations would be strong enough to survive a saccade and affect perception. This question will be tackled in Study IV of this dissertation.

2.5 Aims and approaches

This dissertation aimed to gain understanding on what determines the nature of perception across saccadic eye movements. The theoretical basis for this investigation was that information during the saccade is omitted from perception and that information from before and after a saccade are either integrated into a coherent percept, or segregated in order to detect a potentially relevant change between the pre- and postsaccadic information, and that integration and segregation should be mutually exclusive outcomes of transsaccadic perception. The aim was approached by investigating: 1) transsaccadic integration and how it is influenced by physical discrepancies between pre- and postsaccadic information, 2) transsaccadic segregation and how the ability to detect intrasaccadic target displacements differs between children and adults, 3) the interplay between natural appearance differences across the visual field and the ability to segregate transsaccadic information, and 4) the impact of adaptation to presaccadic stimulation on postsaccadic perception.

In all four studies, we precisely tracked a participant's current gaze position to determine the time when the participant made a saccadic eye movement towards a saccade target presented in the periphery of their visual field on a display. This allowed us to change position or other features of the saccade target and hence insert physical discrepancies between pre- and postsaccadic information. Perception was measured via two-alternative-forced choice tasks in which participants had to categorise their percept into one of two options (e.g., whether a target was circular or triangular; or whether it changed towards a more circular or towards a more triangular shape across the saccade) over various levels of features or feature changes. The level at which participants reported both categories equally often over all trials informed us about their point of subjective equality (PSE), indicating the perceived point of divergence between the two categories (e.g., at a perfect mixture of a triangle and a circle). When intrasaccadic changes had to be categorised, this parameter was renamed "point of subjective stability" (PSS, e.g., at a point when no change was presented). The standard deviation over all perceptual reports provided an

estimate of the just-noticeable difference (JND) of a participant. It indicates the resolution of this perceived feature- or feature change space and is inversely related to the reliability of a percept. For instance, a small JND of 0.1 (within a range between zero and one) would indicate that a stimulus or a stimulus change that represents the PSE or PSS can diverge up to 10% and still be perceived as the category bound. Finally, for change-detection measurements, one can also estimate a detection threshold from the point at which participants categorised the changes correctly above chance level (this is usually 75% correct). A high threshold therefore indicates a low ability to detect changes and a low threshold indicates a high ability to detect changes.

2.5.1 Study I

With the first study of this dissertation, we aimed to investigate the robustness of transsaccadic integration to image changes. The work by Wolf and Schütz (2015) as well as by Ganmor et al. (2015) built the basis for this investigation. The authors found indicators for optimal transsaccadic integration of orientation information in accordance with predictions made by a Maximum-Likelihood Estimation (MLE) model (Ernst & Banks, 2002; Ernst & Bülthoff, 2004). Such predictions are two-fold: 1) the appearance of a stimulus viewed across a saccade should correspond to the weighted sum of the pre- and postsaccadic appearances of that stimulus, and 2) the reliability of the integrated percept should equal the sum of the reliabilities of the pre- and postsaccadic information. We chose to test transsaccadic numerosity perception on these predictions in order to see whether this mid-level information can be integrated across saccades.

Numerosity is the number of individual elements in a stimulus and in the case of our study, the number of dots within a dot cloud. Numerosity appeared to be an interesting visual feature to investigate because estimates of numerosity differ between peripheral and foveal vision: in the periphery participants typically underestimate the number of dots compared to the fovea (Valsecchi et al., 2013). Integrating such distinct appearances into a single appearance is a natural challenge that the visual system should have to face in every-day perception. Additionally, numerosity information could be integrated by the visual system on two distinct levels: on a lower- image-based level as suggested by transsaccadic fusion; or on a higher level where numerosity information is abstracted from the pre- and postsaccadic information and then integrated. A low-level, image-based integration would predict that additionally implemented discrepancies between pre- and postsaccadic information would highly influence transsaccadic integration. For instance, if we shuffled the position of all dots across a saccade, the number of dots should appear higher when pre- and postsaccadic image information is fused; if we swapped the luminance between individual dots across the saccade, a fusion should result in a cancellation of individual dots and thus the number of dots should appear lower. If, however, numerosity integration uses abstracted information, integration should be largely unaffected by those intrasaccadic image changes.

2.5.2 Study II

Study II aimed to investigate how children aged 7 to 12 years differ in their ability to segregate transsaccadic information compared to young adults (19 to 25 years). We approached this aim by investigating the ability to detect intrasaccadic target displacements to the left or to the right on the screen, which usually reveals high thresholds in adults (Bridgeman et al., 1975) but not if a postsaccadic blank is added (Deubel et al., 1996). Children might not integrate separate sources of multisensory information until the age of ten (e.g., Gori et al., 2008; Nardini et al., 2008; but see Negen et al., 2019; Rohlf et al., 2020) which, in turn, might indicate that they show relatively good segregation performance (see also section 4.3) also in transsaccadic perception. This would potentially lead to lower displacement thresholds in children compared to adults.

The findings by Niemeier et al. (2003, 2007) suggested that an opposite difference between children and adults could be expected because the authors demonstrated that higher saccadic uncertainty implies a reduced ability to detect intrasaccadic displacements. That children of a similar age range (5 to 8 years) make larger saccade landing errors (undershoot the target more) than adults has been found before (Munoz et al., 1998; Bucci & Seassau, 2012) but saccade landing variability was not investigated by previous research. However, saccade landing variability is thought to indicate saccadic uncertainty and thus to be an important predictor for the ability to detect intrasaccadic displacements (Niemeier et al., 2003, 2007). Hence, while this study aimed to investigate saccadic suppression of displacement (SSD) in children, it was also our aim to determine their saccade landing accuracy and variability. This was achieved by tracking the gaze position over the course of each trial and by determining a participant's saccade landing position with respect to the presaccadic target location (location on screen before displacement).

The effect of postsaccadic blanking is known to reduce SSD (Deubel et al., 1996) and models on SSD suggests that the influence of saccadic uncertainty is nullified when a sudden blanking of the target indicates that an intrasaccadic change occurred (Niemeier et al., 2003; Atsma et al., 2016). Hence a condition with a postsaccadic blank serves as a suitable way to measure SSD when the potential factor of saccadic uncertainty is eliminated. If uncertainty related to saccades is indeed the driving factor behind potentially stronger SSD in children, SSD in the blank condition should be equal between children and adults, resulting in a stronger blanking effect for children than for adults. Alternatively, if children mandatorily segregate pre- and postsaccadic location information, then there might be no difference between a no-blank and a blank condition within children (small/no blanking effect) and a larger difference between the two conditions within adults (larger blanking effect).

Finally, we aimed to account for the potentially reduced ability in children to deploy sufficiently high degrees of attention to the experimental task (Karatekin, 2004). One approach was to use cartoon animals as target stimuli. Cartoon animals have been suggested

to facilitate the deployment of attention in children to a similar task (Irving et al., 2011). In addition, we embedded the task instructions in a narrative role play in which children took on the role of researchers investigating the "jumping-behaviour" of animals in the jungle.

2.5.3 Study III

In the third study, we aimed to help characterise transsaccadic perception by investigating the interplay between natural appearance differences across the visual field and the ability to segregate pre- and postsaccadic information. Previous literature on transsaccadic segregation i.e., the ability to detect intrasaccadic changes, put a focus on displacement detection (Bridgeman et al., 1975) and comparably few studies have investigated transsaccadic perception of other feature changes (see section 2.3). We chose to investigate transsaccadic perception of the feature shape or specifically, contour curvature. This feature is known to be an important feature for maintaining object continuity (Kayaert et al., 2003; El-Shamayleh & Pasupathy, 2016) and it is known that shape appearance differs between foveal and peripheral vision (Baldwin et al., 2016; Coates et al., 2017; Valsecchi et al., 2018). We speculated that natural differences in appearance across the visual field should facilitate the detection of some intrasaccadic changes but impair the detection of others. For example, if shapes appeared more circular presaccadically than postsaccadically, the discrepancy between pre- and postsaccadic shape information might be larger for physical changes that decreased circularity across saccades; or in other words: an even more circular shape (than physically) would be observed to be followed by a less circular shape.

Alternatively, the visual system might have learned to expect such natural appearance differences and to use this "knowledge" (transsaccadic expectations) to evaluate stability in the environment. As framed by the theory on predictive coding (Rao & Ballard, 1999; Friston, 2009; for a review see de Lange et al., 2018), the future visual input may be predicted based on the current sensory information and crucially on prior knowledge of possible contingencies. Natural transsaccadic contingencies might, for instance, be that objects appear more circular in the periphery before a saccade and less circular in the fovea after a saccade. Based on this knowledge, a prediction for the postsaccadic percept and the error gained from a comparison of this prediction and the actual postsaccadic information might be used to evaluate evidence for or against a possible (but unlikely) intrasaccadic stimulus change. The predictive coding framework suggests, that postsaccadic information further away from the predicted would cause a larger prediction error increasing the likelihood for an intrasaccadic change to be detected. For example, if shapes appear typically more circular in the periphery before a saccade than at the fovea after a saccade, then the visual system might predict a decrease in circularity across a saccade and thus, changes that physically increase circularity across saccades are unexpected and therefore more likely to be detected.

We aimed to investigate these possibilities and also see how such a bias in shape change discrimination would hold with a postsaccadic blank known to facilitate some kinds of shape change perception (Deubel et al., 2002, Experiment 3; Grzeczkowski, van Leeuwen et al., 2020). Therefore, we used shape stimuli that we could morph continually between a more and a less curved shape. Specifically, we morphed shapes between an equilateral triangle and a circle with the medium shape being a Reuleaux triangle (Reuleaux, 1875); shapes that have been successfully used in transsaccadic-learning studies previously (Herwig et al., 2015; Paeye et al., 2018). Our approach was to: a) implement intrasaccadic shape changes (without or with a postsaccadic blank) that either physically increased circularity across saccades or decreased circularity across saccades and let participants indicate the change direction, and b) to show shape information either pre- or postsaccadically and let participants judge the appearance of that shape in comparison to the average shape. By these measures we aimed to compare a potential bias in transsaccadic perception of shape change to appearance differences across the visual field.

2.5.4 Study IV

Study IV investigated whether relatively weak short-term adaptation effects (Foley & Boynton, 1993; Pavan et al., 2012) can persist across a saccade given that a saccade dramatically changes the visual input (Burr & Ross, 1982) and visual processing (for reviews, see Ross et al., 2001; Ibbotson & Krekelberg, 2011; Binda & Morrone, 2018) and hence affect postsaccadic perception in humans. Therefore, we used sinusoidal luminance gratings to induce retinal afterimages and developed a saccade paradigm partly based on the contrast-cancellation method (Kelly & Martinez-Uriegas, 1993). This method implies that a superimposition of the retinal afterimage with a test grating identical to the adapted grating (also referred to as correlated grating) leads to either a weak perception of the afterimage (if the contrast of the test grating is very low) or to a reduced perceived contrast of the test grating (if the contrast of the test grating is higher than that of the after image) or even to the perception of no grating at all if the contrast of the afterimage and that of the test grating cancel each other out. In Study IV we aimed to compare the percept of a same-phase superimposition with a percept when the test grating was of opposite phase to the adapted grating. The phase of an anticorrelated grating should be identical to the afterimage and the two might add up in their contrast such that the resultant perceived contrast is higher than the physical one for the test grating.

We aimed to achieve the simultaneous perception of both cases: the afterimage superimposed on its counterpart (i.e., on the correlated grating) or on its equal (i.e., on the anticorrelated grating). Therefore, we let participants adapt to two vertical gratings which were in phase at some point along the horizontal axis (e.g., both at high luminance) but of opposite phase at another (e.g., one at low, the other at high luminance). Specifically, a slight difference in spatial frequency between gratings meant that by a certain horizontal distance, a full wavelength of one grating could be reached but only half the wavelength

of the other (see Figure 7 for an example). We calculated this critical distance and let participants make a horizontal saccade of that amplitude in between the gratings. By this, we could achieve that the pre- and postsaccadic retinal inputs were partly correlated and partly anticorrelated. During the saccade we aimed to manipulate the contrast difference between the two parts/gratings and let participants indicate which of the postsaccadic gratings had the higher contrast to them. If we found a bias in perceived contrast difference, this would indicate that an afterimage could built up within the presaccadic fixation duration and affect postsaccadic perception.

Our overall approach was to first get a measure of this differential adaptation effect and then use this highly sensitive paradigm to test the temporal limits of luminance adaptation. We intended to continuously reduce the presaccadic adaptation duration in one experiment and to increase the duration between adaptation offset and test-stimulus onset in another experiment. The latter was going to be achieved by inserting a shorter or longer postsaccadic blank-screen period upon saccade onset. By these measures we aimed to determine how rapid and persistent luminance adaptation can be.

3 Study summaries

In this chapter, approaches, methods, the main findings, and the main conclusion for each of the four studies of this dissertation will be summarised. For more detailed information on each study, one may refer to the Publications.

3.1 Study I: Robustness of transsaccadic integration

The first study investigated whether optimal transsaccadic integration applies to numerosity estimation: a) given natural discrepancies between presaccadic peripheral and postsaccadic foveal perception, and b) given additional externally induced discrepancies. To test for optimal (maximum-likelihood) information integration, the mean and the variability of perceptual judgements should be measured and compared to the model predictions. The mean should be the result of an optimal weighting of pre- and postsaccadic information based on their individual reliabilities; the variability of perceptual judgements should be smaller than the variabilities given pre- or postsaccadic information alone. It follows that in order to test those predictions for each participant, perceptual performance had to be measured when only pre or postsaccadic input was provided. Predictions for optimal integration were compared to observed integration performance when stimuli were physically continuous across saccades (Experiment 1), and when the stimuli physically changed global properties intrasaccadically (Experiment 4). Experiments 2 and 3 investigated integration performance for intermediate degrees of intrasaccadic stimulus changes.

In Experiment 1, we addressed the foundational question of whether (physically continuous) numerosity information is integrated across saccades. In a trial, participants had to fixate a central fixation stimulus and execute a saccade towards a peripheral target upon detection. The target could either be a dot cloud with a certain number of dots (numerosity stimulus) or another fixation target. Crucially, the numerosity stimulus was only presented presaccadically in the so-called peripheral condition or solely postsaccadically in the foveal condition. In the integration condition, the numerosity stimulus was presented before and after the saccade (Figure 1A). At the end of each trial, participants had to judge whether the numerosity stimulus contained more or less dots than the average numerosity stimulus estimated throughout the experiment. By fitting a psychometric function to the binary response (more/less) for varying numerosity levels, we could estimate participants' points of subjective equality (PSEs) to determine the mean numerosity estimate in each condition (peripheral, foveal, integration), and their variability (just-noticeable differences, JNDs).

PSEs revealed that numerosity was overestimated in the periphery before a saccade (re-

flected in a negative relative PSE), underestimated in the fovea after a saccade (reflected in a positive relative PSE), and estimated without a bias in the integration condition (Figure 1B). The maximum-likelihood model predicts PSEs for the integration condition to lie between pre- and postsaccadic PSEs; specifically, each single percept should contribute to the integrated percept weighted by its reliability. Reliability was defined as the inverse of the variance of numerosity judgements and hence it was inversely related to the JND (a higher JND indicates lower reliability and vice versa). JNDs were lower overall in the foveal compared to the peripheral condition (horizontal lines in Figure 1C) indicating higher reliability of the postsaccadic foveal percept compared to the presaccadic peripheral percept. Accordingly, the model predicted weights to be higher for the foveal than for peripheral information. We found, however, weights for the peripheral percept to be higher than predicted (Figure 1D). Nevertheless, participants were most precise — had the lowest JNDs — in the integration condition, and observed JNDs were close to predicted JNDs (Figure 1D), which indicates close-to-optimal transsaccadic integration.

Experiment 2 investigated how small local changes between pre- and postsaccadic numerosity stimuli affect integration performance. All trials were similar to the integration condition in Experiment 1, but the degree of intrasaccadic change was manipulated. Either no change was implemented (baseline condition), the position of the dots was changed, or their luminance (from black to white and vice versa). Results showed that participants slightly overestimated numerosity when the dot positions changed across saccades (on average by 2 dots i.e., 4%) but maintained their level of precision in all change conditions compared to baseline and also compared to JNDs from Experiment 1. In summary, results of Experiment 2 suggest that transsaccadic integration occurred despite local intrasaccadic changes to stimulus composition.

In Experiment 3, we took the manipulation of Experiment 2 further to not only apply small local changes such as in individual dot position or luminance, but also apply large global changes that would affect the overall percept of the numerosity stimulus. Therefore, we implemented a strong disproportion of black and white dots in a stimulus (80/20% or 100/0% white or black dots, for an example of 100/0%, see Figure 2A) and again inverted the polarity of each dot across saccades. This manipulation led to a strong change in luminance across a saccade and in a postexperiential questionnaire most participants reported to have detected intrasaccadic changes at least once in this experiment. Nevertheless, integration performance remained close to that of Experiment 1 and JNDs in the change conditions did not differ from JNDs in the respective baseline condition.

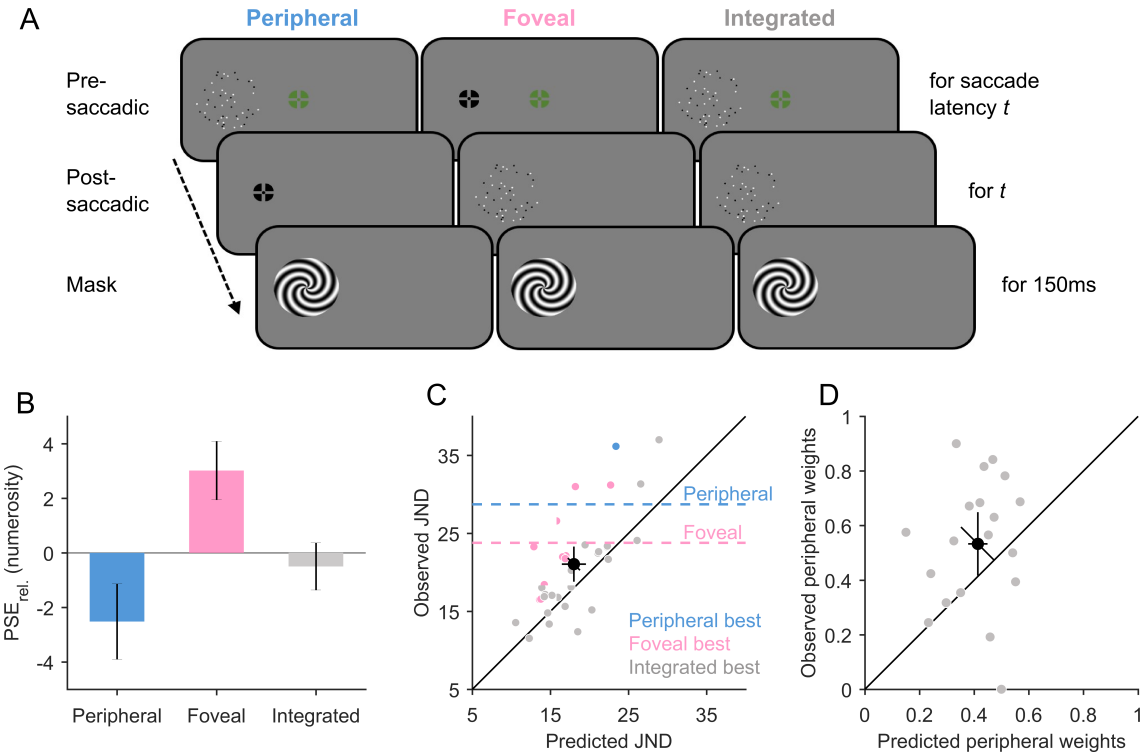

Figure 1. Trial procedure and results Experiment 1 - Study I. A) Schematic trial procedure reduced to essential stimulations for all three conditions (for more detailed procedure plot see Study I - Figure 1). Descriptions on the left show the name of each time window and descriptions on the right indicate the duration of each time window. **B)** Relative PSEs (absolute PSE minus participant's mean PSE) for numerosity estimation over the three conditions tested. Coloured bars indicate the mean over participants and black error bars 95%-confidence intervals. **C)** Observed JNDs over JNDs predicted from the MLE model for the integration condition. The larger black dot with error bars (95%-confidence intervals) shows the mean over participants; smaller dots show individual participant data. Colours of individual data indicate in which condition each participant was most precise. Horizonal dashed lines show the mean JNDs for the peripheral and the foveal condition. **D)** Observed weights of peripheral information (inferred from PSEs) over peripheral weights predicted from the MLE model (inferred from JNDs) for the integrated percept. The larger black dot with error bars (95%-confidence intervals) shows the mean over participants; smaller dots show individual participant data.

As it was surprising that integration was unaffected by object discontinuity, Experiment 4 served as a final verification of this finding. Here, we repeated the procedure from Experiment 1 (including single- and integration conditions) but used only the most disproportional stimuli from the previous experiments (100/0%) and added an integration condition where polarity was inverted intrasaccadically (Figure 2A). The pattern of results for PSEs (Figure 2B) and JNDs (Figure 2C) were similar to that of Experiment 1 and, importantly, integration performance was again close to optimal for numerosity estimation without or with the intrasaccadic change.

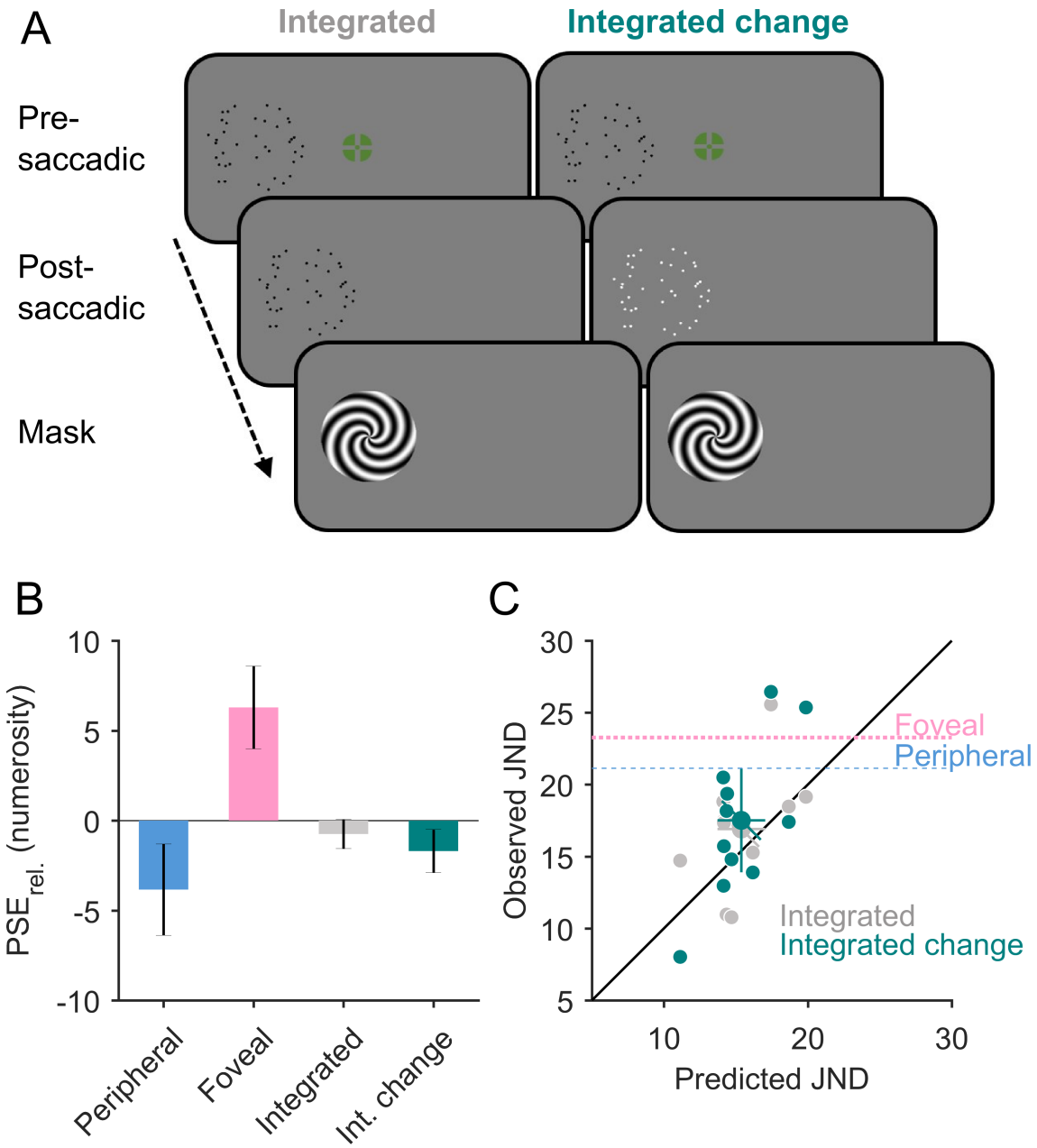

Figure 2. Trial procedure and results Experiment 4 - Study I. A) Schematic trial procedure reduced to essential stimulations for the integrated- (left column) and integrated-change condition (right column). Foveal and peripheral conditions were also tested in this experiment but trial procedures were omitted from this plot for simplicity (see also Figure 1A). **B)** Relative PSEs (absolute PSE minus participant's mean PSE) for numerosity estimation over the four conditions tested. Coloured bars indicate the mean over participants and black error bars 95%-confidence intervals. **C)** Observed JNDs over JNDs predicted from the MLE model for both integration conditions. Larger dots with error bars (95%-confidence intervals) show the mean over participants; smaller dots show individual participant data. Horizonal dashed lines show the mean JNDs for the foveal and the peripheral condition.

In sum, the results of Study I indicate that pre- and postsaccadic numerosity information is integrated across saccades: a) despite natural discrepancies between presaccadic peripheral and postsaccadic foveal perception, and b) even despite stark physical discrepancies implemented during a saccade. This study revealed that close-to-optimal transsaccadic integration is a robust phenomenon when it comes to numerosity estimation. This integration likely serves not only a continuous and stable perception across eye movements but also a more precise numerosity estimation compared to foveal vision alone.

3.2 Study II: Development of transsaccadic segregation

The second study turned towards transsaccadic segregation and the question of how it develops from childhood to adulthood. To this end, we implemented a classic saccadic-suppression-of-displacement (SSD) paradigm to test children's and adults' abilities to segregate pre- and postsaccadic location information. Further, we evaluated each group's intrinsic uncertainty on their saccadic eye movements and how it influences transsaccadic segregation performance.

The following hypotheses were inferred from previous literature: if children have higher saccadic uncertainty compared to adults, they should also have a higher tendency to miss displacements because discrepancies between pre- and postsaccadic location information might rather be assigned to internal (and not external) causes (Niemeier et al., 2003; Atsma et al., 2016). Assuming that the influence of saccadic uncertainty is nullified when a postsaccadic blank is added (Niemeier et al., 2003), children might also show a larger blanking effect than adults. Alternatively, children might show weaker SSD — i.e., a better ability segregate, as their ability to integrate separate sources of information may not yet have fully developed (Gori et al., 2008; Nardini et al., 2008; for a review see Ernst, 2008) and inability to integrate might automatically imply segregation as being the alternative perceptual outcome (for discussion see section 4.3).

To test these hypotheses, we measured SSD in children (7 to 12 years) and young adults (19 to 25 years) with or without a postsaccadic blank. In each trial, participants had to fixate a central fixation stimulus on a screen and initiate a saccade towards a target in their periphery upon detection (Figure 3A). The physical location of the saccade target was manipulated by a left- or rightward displacement either immediately upon online saccade detection, or after a short preceding blank-screen period (blank condition). At the end of each trial, participants had to report whether the target jumped to the left or right during their saccade.

Results revealed that children showed less segregation overall as they were less precise than adults at detecting displacements (higher JNDs, Figure 3B). Interestingly, children showed a larger segregation improvement from the no-blank to the blank condition compared to adults. The first result indicates that children tend to not segregate pre- and postsaccadic information, even when displacements are relatively large. This, together

with the larger blanking effect in children might hint at the underlying cause for the SSD difference between age groups: children might have higher saccadic uncertainty (suggested by the first hypotheses mentioned above).

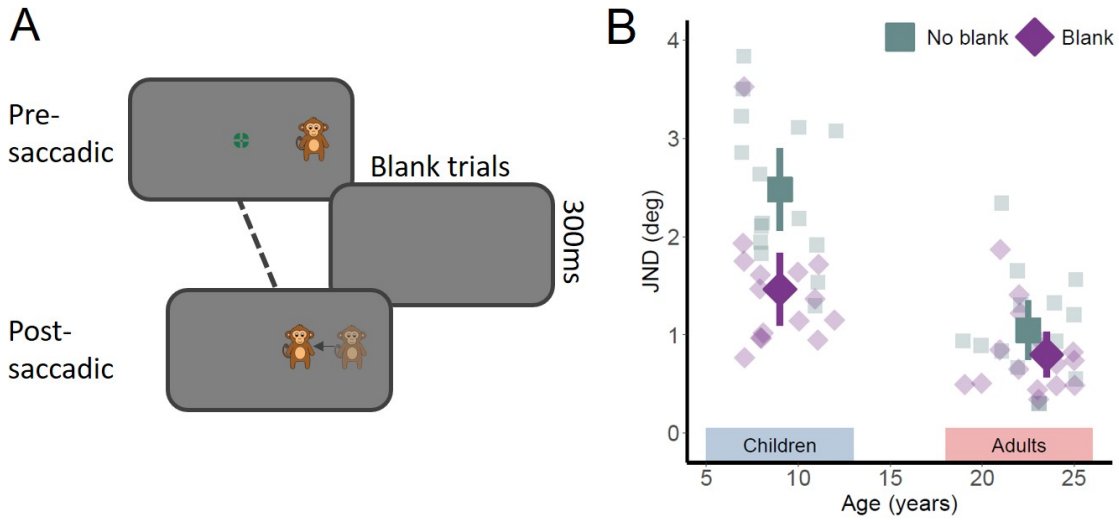

Figure 3. Trial procedure and perceptual results for Study II. A) Trial procedure reduced to main stimulations (for a more detailed procedure plot see Publications - Study I — Figure 1A). A central fixation stimulus was fixated until a saccade target appeared (here to the right of fixation) to which a saccade was initiated (presaccadic time window). Blank trials: 50% of trials contained a 300ms blank-screen period that was initiated upon saccade detection. Either upon saccade detection (no-blank trials) or after the blank duration (blank trials) the postsaccadic position of the saccade target was displayed for 400 milliseconds (postsaccadic time window). Participants gave their response after the postsaccadic stimulus was removed. **B)** JNDs in degrees of visual angle for the no-blank (turquoise squares) and blank condition (purple diamonds) over age groups. Individual participant data is shown in small symbols and means in larger symbols with error bars as 95%-confidence intervals. Mean symbols for adults are offset on the horizontal axis to avoid overlap; they do not reflect mean age.

We further deduced saccadic uncertainty from the participants' saccade metrics. Saccade landing distributions (Figure 4A) revealed that children were more likely to undershoot the target (less accurate) but their landing positions were also more variable than those of adults (less precise). In addition, children showed longer saccade latencies but subsequent corrective saccades were initiated faster than by adults (Figure 4B). Taken together, these differences in saccade metrics may be taken as evidence that children have higher uncertainty with respect to their saccadic eye movements. Hence, larger and more variable saccade landing errors may be expected by their visual system resulting in an increased readiness to correct suboptimal landing positions.

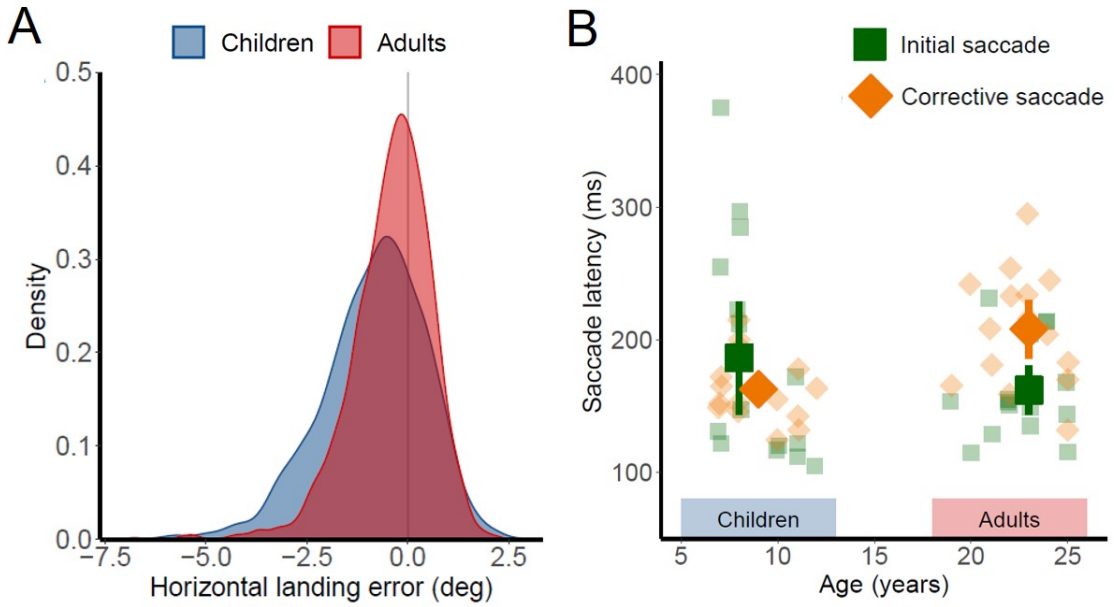

Figure 4. Saccade metrics for Study II. A) Probability density for horizontal landing error in children (blue) and adults (red). The vertical line at zero represents the presaccadic horizontal target position and negative values represent undershooting of the saccade target. **B)** Saccade latencies for initial saccades (green squares) and corrective saccades (orange diamonds) over age groups. Individual participant data is shown in small symbols and means in larger symbols. Mean symbols for children are offset on the horizontal axis to avoid overlap; they do not reflect mean age. Error bars show 95%-confidence intervals.

With Study II we found that children show stronger saccadic suppression of displacement with or without a postsaccadic blank compared to adults. However, children also showed a stronger reduction of SSD due to a postsaccadic blank compared to adults (larger blanking effect). The finding that saccades of children were less accurate, less precise, and corrected faster compared to that of adults may be taken as evidence for higher saccadic uncertainty in children. In conclusion, the ability to segregate transsaccadic information develops across the life span from childhood to adulthood and may be based on motoric and perceptual capabilities, which the visual system seems to take into account to guide perception.

3.3 Study III: Expectations for transsaccadic information

The third study aimed to further characterise transsaccadic segregation to gain more understanding about its underlying mechanisms. Therefore, transsaccadic perception of the stimulus feature shape, specifically, contour curvature was investigated: how it is perceived pre- and postsaccadically, and how those potential appearance differences across the visual field influence intrasaccadic shape change detection.

Shape stimuli were morphed between a triangle and a circle in ten steps with a parameter k indexing shape curvature (Figure 5A). In a change-discrimination task (experimental part A), two different change directions of varying magnitudes were presented: circularity decrease (e.g., from shape $k_{pre} = 1$ to $k_{post} = 0.6$) or circularity increase (e.g., from shape $k_{pre} = 0.2$ to $k_{post} = 0.6$); participants had to indicate which change direction they perceived. In a shape-discrimination task (experimental part B), a shape was either exclusively presented presaccadically in the periphery, or postsaccadically at or around the fovea (procedure similar to peripheral and foveal trials in Figure 1A) and participants had to indicate whether this shape was more circular or more triangular than the estimated average shape. In the first experiment (composed of part A and B), we investigated transsaccadic segregation for shape with or without a postsaccadic blank and its interaction with visual-field differences. The second experiment was conducted to narrow down potential factors contributing to an observed bias in shape change perception.

In Experiment 1A, a saccade target stimulus appeared in the periphery of the visual field and changed its shape either immediately upon detection of a saccade towards it (no-blank condition), or after a preceding 200ms blank-screen period (blank condition) and remained on screen for half the presaccadic stimulus presentation time. Change discrimination accuracy (PSS: point of subjective stability, showing a potential bias) and precision (JNDs, showing a potential blanking effect) were evaluated based on the binary judgements. To test shape appearance in Experiment 1B, a shape stimulus was either presented in the periphery before a saccade that turned into an uninformative fixation stimulus at the fovea after the saccade (presaccadic condition), or this order was inverted such that the informative shape stimulus was solely available after the saccade (postsaccadic condition). Natural differences in shape appearance across the visual field could be expected according to previous literature (Baldwin et al., 2016; Coates et al., 2017; Valsecchi et al., 2018); leaving the possibilities that with our stimuli, shapes might either appear on average more circular or more triangular in the periphery compared to the fovea. These differences might perceptually magnify a certain intrasaccadic change direction leading to higher detection rates for the respective change direction, i.e., to a bias in change perception. Alternatively, visual-field differences might have been learned by the visual system and those expectations might be used to evaluate external stability. In this case, expectations on a typical transsaccadic appearance change should increase detection rates for physical changes that contradict expectations.

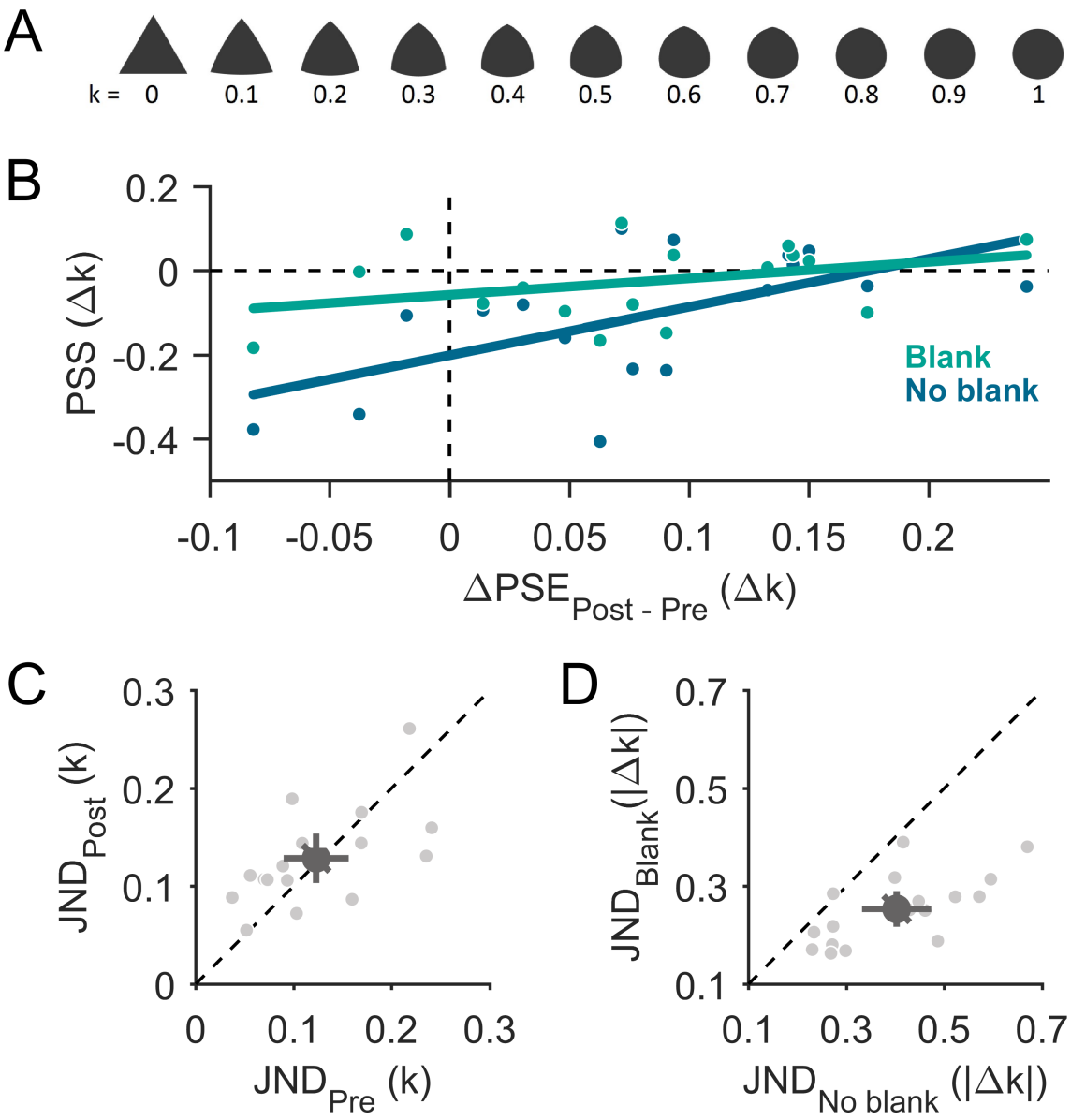

Figure 5. Stimuli and results of Experiment 1 - Study III. A) All shape stimuli with curvature index k going from zero (triangular, T) to one (circular, C). Circumradii of shapes were adjusted to keep the covered area approximately constant across shapes. **B)** The effect of individual appearance differences between pre- and postsaccadic shape perception (difference of PSEs from Experiment 1B, horizontal axis) on the bias in the change-discrimination task (PSS from Experiment 1A, vertical axis) separately for the blank (green) and no-blank condition (blue). The more positive a PSE difference, the stronger a bias for perceiving shapes as more circular presaccadically and the more negative a PSS, the stronger was the bias for circularity-increase changes. Linear correlation fits for each blanking condition are represented by the coloured solid lines. **C)** JNDs compared between pre- and postsaccadic conditions in Experiment 1B. **D)** JNDs compared between blanking conditions in Experiment 1A. **C & D)** Light-grey dots represent individual participant data and the dark-grey dot indicates the overall mean. The error bars indicate 95%-confidence intervals within each condition (cardinal bars) or between conditions (oblique bar).

Results of Experiment 1 revealed a bias for shape-change perception — changes that increased circularity across saccades were more likely to be detected (indicated by negative PSS in Figure 5B). Shape appearance was also biased — participants perceived shapes on average as more circular presaccadically than postsaccadically (indicated by positive ΔPSEs in Figure 5B). At the same time, variability in reporting pre- and postsaccadic percepts was approximately equal (Figure 5C). An interaction between the change-direction and appearance biases can be seen in the positive correlation shown in Figure 5B. The more pronounced the pre-/postsaccadic appearance difference was for a participant, the smaller was their bias for circularity-increase changes. These results suggest that both of the above-mentioned hypotheses apply. Appearance differences seem to have magnified the change direction for circularity decrease and circularity-increase changes were predominantly detected, a direction that is opposite to a potentially typical transsaccadic appearance of circularity decrease. These effects may hint at a direct as well as an indirect influence of visual field differences on transsaccadic perception. PSS estimates for the blank condition, on the other hand, were shown to be largely unaffected by these factors (Figure 5B), probably because there was overall less uncertainty with a postsaccadic blank (Figure 5D).

The correlation shown in Figure 5B can only be due to a perceptual phenomenon; nevertheless, a response bias cannot be excluded to have influenced and to have partially led to the change-direction bias in Experiment 1A. A second experiment was designed to control for this possibility. Experiment 2 was similar to Experiment 1, except two shape stimuli were displayed simultaneously and a saccade had to be made towards a central fixation stimulus between the two. In the change-discrimination task (part A), one of the shape stimuli changed during the saccade (Figure 6A) and participants had to report where the change occurred (top or bottom). By this design we could calculate detection thresholds (75%-correct responses) for each change direction. In the appearance task (part B), the shape stimuli were identical and participants should again compare the pre- or postsaccadic shape of the current trial to the overall mean shape.

Results showed that detection thresholds were significantly lower for the circularity-increase change direction compared to circularity decrease (Figure 6B). This confirms that there is a perceptual bias to preferentially detect circularity increases across saccades. Appearance biases (Figure 6C) measured in Experiment 2B were also similar to the ones found in Experiment 1B; remarkably, even though quite different stimulus eccentricities (e.g., 15° versus 5° of visual angle in presaccadic vision) and a new group of participants were tested.

In summary, Study III revealed that transsaccadic perception of shape changes is biased, as changes that increased circularity across saccades were detected more often. In addition, shapes seem to appear more circular in presaccadic vision compared to postsaccadic vision. Those appearance differences across the visual field can explain the change-direction bias

in terms of an indirect effect of transsaccadic expectations. In conclusion, transsaccadic segregation of shape information may be based on a predictive mechanism.

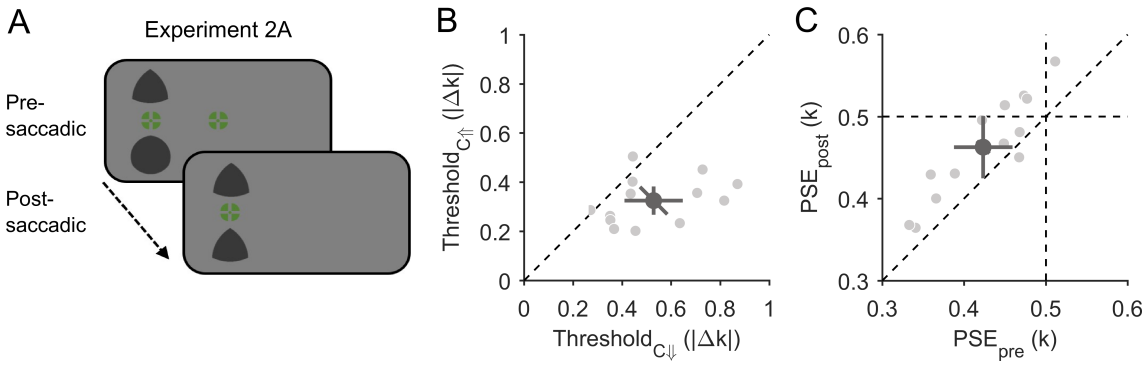

Figure 6. Trial procedure and results Experiment 2 - Study III A) Schematic trial procedure reduced to essential stimulations in Experiment 2A showing an example for a circularity-decrease change across a saccade. Upon postsaccadic stimuli offset, participants had to indicate the location (top or bottom) of the change. **B)** Change detection thresholds for circularity-decrease changes (C↓, horizontal axis) compared to circularity-increase changes (C↑, vertical axis) for Experiment 2A. **C)** PSEs (shape appearance) compared between pre- and postsaccadic vision. PSEs below 0.5 indicate a bias for over-proportionally often judging shapes to be more circular. Data points above the dashed diagonal line indicate a less circular appearance in the postsaccadic condition compared to the presaccadic condition. **B & C)** Light-grey dots show individual participant data and the dark-grey dot indicates the overall mean. The error bars indicate 95%-confidence intervals within each condition (cardinal bars) or between conditions (oblique bar).

3.4 Study IV: Persistence of presaccadic adaptation

With Study IV, we investigated how basic mechanisms in neuronal information processing can influence transsaccadic perception. Specifically, we addressed the question of whether neuronal adaptation that built up during brief presaccadic fixation periods can affect postsaccadic perception. It is known that prolonged adaptation ($\geq$ 3s) can survive a saccade (e.g., Knapen et al., 2009; Knapen et al., 2010) but we were interested in whether adaptation below this duration or even within the range of natural fixation durations (200 – 300ms) can be strong enough to persist across a saccade.

We developed a saccade-specific contrast-discrimination paradigm in which one half of a retinal afterimage was superimposed with a correlated luminance stimulus, which should lead to perceived-contrast reduction (contrast-cancellation method, Kelly & Martinez-Uriegas, 1993) and the other half with an anticorrelated luminance stimulus, which should increase the perceived contrast. A demonstration of this effect can be found in Figure 7. At the onset of a trial, participants adapted to two gratings — one filled the upper and the other filled the lower half of the screen — while fixating between them. Upon detection of a saccade target to the left or to the right, participants made a saccade

towards it. During the saccade, the relative and mean contrast of the two gratings was changed and the postsaccadic stimulus was masked after 400ms presentation duration (Figure 8A). Crucially, the saccade target location was chosen such that the retinal image belonging to one grating inverted its pattern (white became black and vice versa) across the saccade (anticorrelated grating) and the other stayed unchanged (correlated grating). Participants had to report which grating (upper or lower) had the higher contrast. If short-term presaccadic luminance adaptation affects postsaccadic contrast perception, physical contrast differences between the postsaccadic gratings Δc ($\Delta c = c_{anti}$ - c_{corr}) should be mis-perceived. Specifically, the anticorrelated grating should be disproportionally often perceived as being of higher contrast than the correlated grating, leading to a (negative) shift in the point of subjective equality (PSE).

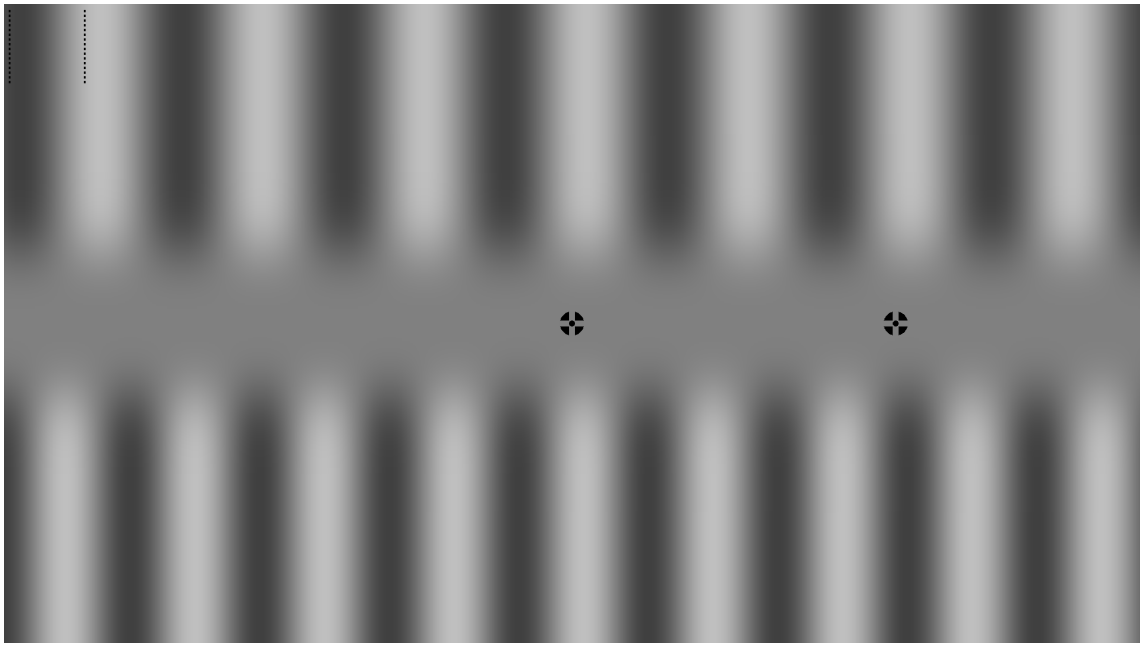

Figure 7. Demonstration of manipulation of Study IV. To reproduce appropriate spatial frequencies, one should view the image approximately at a distance of an arms lengths and adjust the size of the image such that one's thumb placed on the image fits approximately in between the two dashed lines in the top left corner of the image. The described effect can be experienced by steadily fixating the central fixation stimulus for a few seconds, or until the gratings begin to fade (to achieve the largest possible effect), and subsequently shifting gaze onto the second fixation stimulus to the right. While fixating the second fixation stimulus, one should observe the top-half grating to be of lower contrast (correlated grating) than the bottom-half grating (anticorrelated grating). When the second fixation stimulus is fixated steadily, with low variance in gaze position, the effect can be observed for a long duration.

The first experiment was conducted to provide a baseline measure of the effect. Therefore, various levels of postsaccadic contrast differences were tested with an average adap-

tation duration of around 1.7 seconds. Results showed a strong and reliable shift in PSEs indicating a higher perceived contrast of the anticorrelated grating (Figure 8B).

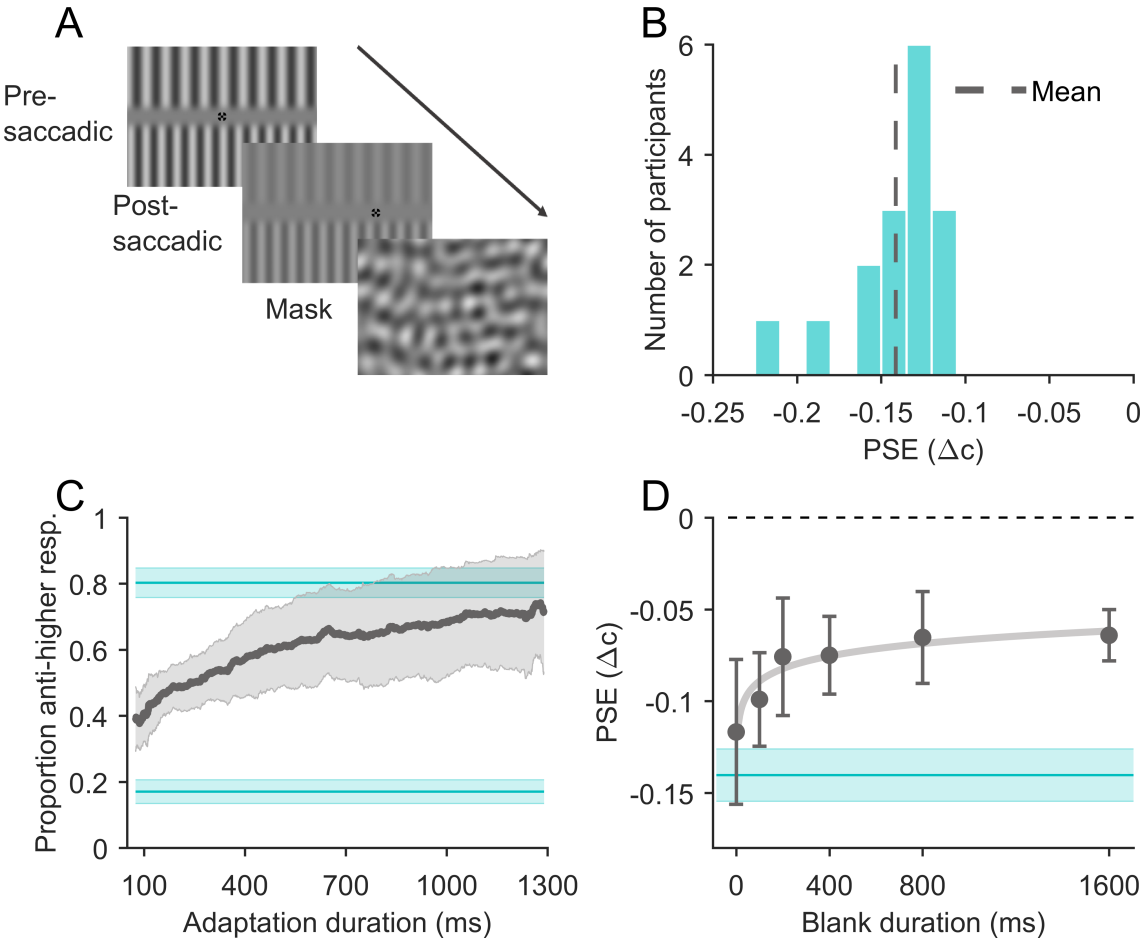

Figure 8. Trial procedure, and results of Experiments 1 to 3 - Study IV. A) Schematic trial procedure showing presaccadic stimulation (adaptation phase, until saccade onset), postsaccadic stimulation (test phase, 400ms duration) and mask (300ms duration). **B)** Histogram of PSEs from the main experiment (Experiment 1). A negative PSE indicates a higher perceived contrast of the anticorrelated grating. The dashed line shows the mean PSE over participants. **C)** Results of Experiment 2: proportion responses judging the anticorrelated grating to be of higher contrast over adaptation durations. The dark-grey line shows the mean over participants. The upper turquoise line shows the expected mean proportion of responses given the average PSE from Experiment 1. The lower turquoise line shows the expected mean proportion of responses assuming a PSE at zero Δc (no adaptation effect). **D)** Results of Experiment 3: PSEs over postsaccadic blank durations tested. Dots represent means over participants and error bars the 95%-confidence intervals. The grey line represents the logarithmic function fitted to the mean data. The turquoise line shows the mean PSE from Experiment 1. **C & D)** All shaded areas show 95%-confidence intervals.

Given the robust baseline effect from Experiment 1, we tested its limits as we varied the adaptation duration between approximately 100 milliseconds and 1.3 seconds. In this

second experiment only one level of contrast difference was tested ($c_{anti} < c_{corr}$) and the proportion of responses that indicated the anticorrelated grating to be of higher contrast was analysed. For comparison, we estimated the proportion of anticorrelated-higher responses that would correspond to no adaptation effect from the data of Experiment 1 (PSEs were set to zero for fitting). Strikingly, the proportion of anticorrelated-higher responses was already above this estimated baseline for the shortest adaptation durations tested (Figure 8C).

Experiment 3 was conducted to test the temporal persistence of the transsaccadic adaptation effect. Design and procedure were similar to Experiment 1 except that a blank-screen period preceded the postsaccadic stimulus. This period was varied between zero- and 1.6 seconds in exponential steps, and multiple contrast-difference levels were tested allowing for estimation of PSEs for each blank duration. We found the adaptation effect to decay (increasing PSEs) with increasing blank durations but in a logarithmic fashion: not reaching zero even after the longest delay (Figure 8D).

In a final experiment (Experiment 4), we investigated to what extent different parts of the visual field contributed to the adaptation effect. To this end, the stimulation during adaptation was similar to that of Experiment 1 but perception in different parts of the visual field was tested after the saccade. The postsaccadic gratings were partially covered by a mask stimulus reducing them to a small vertical section (Figure 9A) that was either positioned around the postsaccadic centre of gaze or around the screen centre further out the periphery. The results indicate that adaptation affected postsaccadic perception in both sections of the visual field but clearly to different extents: the adaptation effect around the centre of gaze was roughly four times higher than that measured in the periphery (Figure 9B), while discrimination precision was approximately equal for both conditions (Figure 9C). This might indicate that foveal neurons (presumably retinal ganglion cells) contributed most to the adaptation effect.

In sum, we found that short-term luminance adaptation affected contrast perception after a saccade. This effect emerged rapidly within a few hundreds of milliseconds, decayed slowly in a logarithmic fashion, and was mostly driven by perception around the centre of gaze. Study IV demonstrates that short-term adaptation during natural fixation durations is strong enough to influence postsaccadic perception.

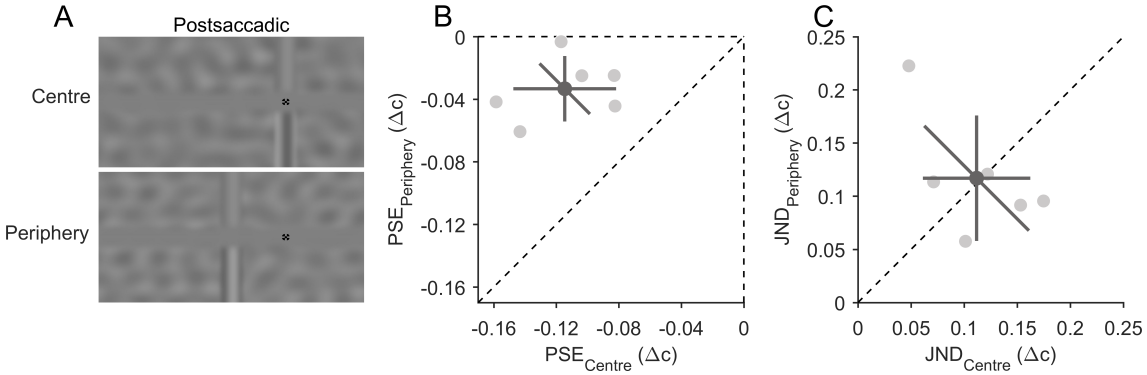

Figure 9. Postsaccadic stimuli and results of Experiment 4 - Study IV. A) Example postsaccadic test displays presented to a participant in Experiment 4 for when the test-stimulus slice was presented around the centre of gaze (upper panel) or to the periphery (lower panel). **B)** PSEs compared between the slice-at-centre condition (horizontal axis) and slice-in-periphery condition (vertical axis). Data points above the dashed vertical line indicate a stronger adaptation effect for when the test-stimulus slice was presented around the centre of gaze. **C)** JNDs compared between the slice-at-centre condition (horizontal axis) and slice-in-periphery condition (vertical axis). Data points on the diagonal dashed line indicate that participants were equally precise in both conditions. **B & C)** Light-grey dots show individual participant data and the dark-grey dots show the means over participants. The error bars indicate 95%-confidence intervals within each condition (cardinal bars) or between conditions (oblique bars).

4 Discussion

The studies underlying this dissertation investigated the robustness of transsaccadic integration (Study I), the development of transsaccadic segregation (Study II), expectations about transsaccadic information (Study III), and the persistence of presaccadic adaptation (Study IV).

The first study investigated whether visual information on numerosity, that is distinct across the visual field and saccades, is integrated optimally across saccades. Responses based on pre- and postsaccadic information available across a saccade were more precise and more accurate than responses based on pre- or postsaccadic information alone. Compared to predictions for optimal cue integration (from MLE model), performance was close but not similar to performance predicted. Participants' performance remained at this level when we induced small (local) and large (global) task-irrelevant feature changes during saccades. It can be concluded that close-to-optimal transsaccadic integration of numerosity information is largely resistant to task-irrelevant feature changes.

The second study investigated whether and how the visual system segregates transsaccadic information at childhood compared to adulthood and examined possible contributions of saccadic uncertainty to intrasaccadic displacement detection. We found that children detected intrasaccadic displacements less precisely than adults indicating greater saccadic suppression of displacement in children. This was accompanied by a larger blanking effect in children as they benefited more from a postsaccadic blank than adults. Saccade parameters revealed that children made less accurate and less precise saccades than adults and initiated corrective saccades more rapidly than adults; all three findings may be attributed to higher saccadic uncertainty in children. The main conclusion that may be drawn is that the tendency to segregate transsaccadic information increases from childhood to adulthood and that this might be determined by expectations about self-induced errors on postsaccadic location information.

The third study further examined the role of transsaccadic expectations by looking at the relationship between shape-change discrimination performance and pre- and postsaccadic shape appearance. We found that changes were detected more easily when shapes became more circular during a saccade compared to when they became more triangular. Overall appearance of our shape stimuli was more circular before the saccade in the periphery than after the saccade at or around the fovea. The most plausible interpretation of these results may be that transsaccadic appearance differences that are typically experienced (circularity decrease) generate respective transsaccadic expectations. A change direction

that is opposite to an expectation (circularity increase) may elicit a large error facilitating change detection.

The fourth study investigated whether postsaccadic perception can be affected by short-term presaccadic adaptation. We found strong and persistent luminance-adaptation effects on postsaccadic contrast perception that built up within a few hundreds of milliseconds. These findings suggest that short-term adaptation, even within natural fixation durations, can affect perception after saccades.

In the following sections, I will discuss the findings of these studies in light of the current literature. I will also evaluate the prevailing theories on transsaccadic perception and visual stability in the light of these four studies.

4.1 Prerequisites for transsaccadic integration

What are the prerequisites for transsaccadic integration to occur? There are overarching information-processing resources needed for transsaccadic integration such as memory (Stewart & Schütz, 2018b; Kong et al., 2021) and attention (Stewart & Schütz, 2018a; Kong et al., 2021); nevertheless, it requires relatively little time as it can happen very rapidly within a few tens of milliseconds of stimulus observation (Fabius et al., 2016; Stewart & Schütz, 2019). In the following subsections I will elaborate on further aspects that are believed to be requisites for transsaccadic integration.

4.1.1 Object continuity

Object continuity, that is keeping track of an object's identity, is one of the fascinating achievements of visual perception considering that object information is frequently displaced across the retina. According to the model by Atsma et al. (2016), the assignment of pre- and postsaccadic information to be due to the same cause and hence to belong to the same object identity, is relevant for integration to occur. The model implies that physical discrepancy between pre- and postsaccadic information should decrease the likelihood of integration. Although the authors considered task-relevant location information to be used for causal inference only, other features are likely to guide transsaccadic perception as well. For example, accompanying changes in object form or luminance can facilitate the detection of intrasaccadic displacements (Demeyer et al., 2010a; Tas et al., 2012). Accordingly, any physical discrepancy between pre- and postsaccadic information might hinder transsaccadic integration.

At the same time, some physical discontinuity does not seem to hinder transsaccadic integration. In Study I, we showed that close-to-optimal reliability enhancement occurs even when large physical discrepancies are implemented between pre- and postsaccadic numerosity stimuli. This finding is in contradiction with an assumption that discrepancies between pre- and postsaccadic information impair transsaccadic integration. It might be, that discrepancies regarding the task-relevant feature (numerosity as opposed to luminance

or dot position) solely, are used to inform causal inference. However, this would not explain why better segregation performance could be observed with task-irrelevant feature changes in previous studies (Demeyer et al., 2010a; Tas et al., 2012). Alternatively, some feature changes may be more expected to change at a short time scale than others and therefore, are given a lower weight when evidence for or against a common cause is evaluated. For instance, luminance changes might occur more frequently in everyday perception than changes in the number of static objects.[1]

In this line of thought, one should also consider that physical continuity does not imply perceptual continuity. Physically identical pre- and postsaccadic information can be perceived differently due to visual-field differences as we showed with Study I for numerosity and with Study III for shape. These natural biases should also be weighted according to the reliabilities of the information they are based on; this is approximately the case for numerosity as we demonstrated in Study I (see also subsection 4.1.3). Visual-field differences may affect one feature dimension more than another and presumably in a reoccurring fashion such that the visual system can expect typical changes in a feature dimension. This is particularly evident given the results of Study III, indicating that shape changes that are opposite to what visual-field differences would typically cause, are more likely to be segregated. Hence, a causal inference model might apply for transsaccadic perception but the underlying evaluation-of-evidence process requires additional informational sources. These may be based on transsaccadic expectations, which should be specific to every visual feature available in the stimulus.

4.1.2 Predictive remapping

Predictive remapping may be a neuronal mechanism mediating transsaccadic integration (for reviews, see Melcher & Colby, 2008; Higgins & Rayner, 2014). Specifically, the time course of transsaccadic information processing investigated by Wolf and Schütz (2015) suggests that peripheral information is collected in peripheral neurons before the saccade and then transferred to foveal neurons around the time of the saccade. Effects of increased attention at the future (postsaccadic) retinotopic location of a target before saccade onset have been linked to remapping (Rolfs et al., 2011; for a review see Rolfs, 2015). In turn, transsaccadic integration seems to rely on the allocation of attention (Stewart & Schütz, 2018a). It has been, however, a matter of debate whether remapping transfers also feature information about the target i.e., whether the pre-activation of foveal neurons is nonspecific and solely corresponds to a shift of attention pointers (e.g., Knapen et al., 2009; Knapen et al., 2010; Cavanagh et al., 2010) or whether feature information is also remapped (e.g., Melcher, 2007, 2008; Harrison et al., 2013; D. He et al., 2017). The most recent studies suggest that there is feature-specific information remapped across saccades (T. He et al., 2018; Ge et al., 2021).

[1] One may simply picture standing in the shadow of a tree when its leaves and therefore the shadow of its leaves is constantly moved by the wind.

Findings of Study I suggest that for transsaccadic numerosity perception, it is not low-level feature information (such as luminance) that is integrated, but abstracted numerosity information only, indicating that numerosity integration occurs in higher or mid-level visual areas. Mid-level visual processing areas located in the parietal cortex have been associated with the perception of numerosity during fixation (e.g., Piazza et al., 2004; Piazza et al., 2007; Harvey et al., 2013; for reviews, see Nieder & Dehaene, 2009; Piazza & Izard, 2009). Fittingly, remapping was found in the lateral intraparietal area (Duhamel et al., 1992) and is also known to be a property of neurons in V3 and V4 (Nakamura & Colby, 2002; Merriam et al., 2007), which are mid-level visual processing areas located in the parietal cortex. Interestingly, transsaccadic processing seems to occur in parietal cortex also for lower-level features such as orientation (putative V4, Dunkley et al., 2016) and spatial frequency (putative V3, Baltaretu et al., 2021). In addition, disrupting information processing by transcranial magnetic stimulation over parietal cortex has been shown to impair transsaccadic memory for orientation (Prime et al., 2008). In summary, predictive feature remapping is likely a requisite for transsaccadic integration, and transsaccadic processing for several visual features seems to happen in an area known to show remapping: the parietal cortex.

4.1.3 Reliability estimation

For separate sources of information to be integrated in an optimal way, each information source needs to be weighed by its reliability (Ernst & Bülthoff, 2004). The question is: what informs the system about the reliability of a signal? Recent studies demonstrated that perceptual uncertainty is directly related to the noise in sensory encoding — i.e., to the width of the probability distribution generated by encoding neurons (van Bergen et al., 2015; van Bergen & Jehee, 2019). Interestingly, van Bergen and Jehee (2019) also showed that integration of past and present information reduces uncertainty (as identified by neuronal noise), which is in line with predictions from maximum likelihood estimation (reliability enhancement). Even though this evidence suggests that uncertainty relates directly to sensory encoding and should hence be reflected in JNDs, the MLE predictions based on JNDs underestimated the contribution of peripheral presaccadic information to transsaccadic perception in Study I (Figure 1D). Specifically, less reliable peripheral information seems to have influenced the average integrated percept more than the more reliable postsaccadic foveal information. This is not only suboptimal in regard to the MLE model but also opposite to the previously observed deviations from optimal weighting, where the contribution of foveal information was found to be higher than predicted by the MLE model (Ganmor et al., 2015; C. Wolf & Schütz, 2015). An additional, unusual finding we observed is that numerosity was underestimated postsaccadically at the fovea but overestimated presaccadically in the periphery. Previous literature found that numerosity is underestimated in peripheral compared to foveal vision (Valsecchi et al., 2013). Especially since presaccadic perception should be influenced by the execution of a saccade,

for instance due to a transsaccadic prediction (e.g., Herwig & Schneider, 2014; Valsecchi & Gegenfurtner, 2016), by pre-saccadic enhancement of spatial resolution (H.-H. Li et al., 2016; H.-H. Li et al., 2019), or reduction of visual crowding (Harrison et al., 2013), it should be kept in mind that Study I and the study by Valsecchi and colleagues (2013) measured substantially different aspects of vision. That visual-field differences measured with or without saccades are not equivalent should also be considered when one wants to compare pre- and postsaccadic shape estimates found in Study II with peripheral and foveal shape perception measurements (Baldwin et al., 2016; Coates et al., 2017; Valsecchi et al., 2018).

Nevertheless, the underestimation of numerosity we found for postsaccadic foveal vision could also be due to methodological differences beyond saccade execution. For instance, concerning available stimulus-observation time: postsaccadic presentation in each trial of Study I equalled the presaccadic presentation duration of that trial which depended on a participant's saccade latency and was around 200 milliseconds on average. In addition, to prevent any further processing beyond presentation duration, postsaccadic stimuli were followed by a mask (Figure 1A). A recent study by Cheyette and Piantadosi (2020) convincingly demonstrates that observation time is a crucial factor for numerosity estimation, especially for high numerocities such as we used in Study I. The authors suggest that the encoding of higher numerosities requires more time as this visual information is to some extent processed sequentially (in chunks of information). Accordingly, numerosity estimates may increase over time instead of being instantaneous, leading to underestimation with decreasing observation time. It is likely that the brief processing time of around 200 milliseconds led to the underestimation in foveal trials in contrast to peripheral trials because processing of visual information is substantially faster at larger eccentricities (Carrasco et al., 2003). An alternative reason may be inferred from the theoretical implications postulated in Study III: when perceived numerosity truly increases towards the fovea (Valsecchi et al., 2013) transsaccadic expectations of numerosity increase might have influenced presaccadic perception in peripheral trials (numerosity was estimated higher due to the integration with a high-numerosity prediction) but such a prediction was not available to prepare postsaccadic perception in foveal trials as there was no presaccadic numerosity stimulus to trigger predictions.

Taken together, the underestimation of presaccadic peripheral weights by MLE in Study I might indicate that either reliability estimation from JNDs is not fully representative of the true uncertainty or that the PSE estimate for foveal vision does not reflect the true numerosity percept in a transsaccadic condition under certain circumstances. Important circumstances may be an imbalance between time provided and time needed to process stimulus information. The estimation of whether there was enough time to encode the stimulus i.e., the abruptness of encoding termination (a steep decrease in processing instead of a shallow one) could be an additional information source for uncertainty estimation. As in Study I, this might have led to the down-weighting of postsaccadic numerosity

information regardless of superior precision of postsaccadic numerosity estimates. This aspect of uncertainty estimation has not been investigated by the studies mentioned above and might be of interest for future investigations. In addition, it might be desirable to disentangle the contribution of transsaccadic predictions to pre-, post-, and transsaccadic perception and whether their influence is partly omitted by design when testing presaccadic or postsaccadic perception alone.

4.2 Adaptation in transsaccadic perception

Another potential problem concerning the measurement and comparison of pre- and postsaccadic perception might be suggested by the results of Study IV showing that short-term luminance adaptation within a few hundred milliseconds can influence postsaccadic perception. Specifically, a pattern of luminance stimulation on the retina attenuated perceived contrast of a postsaccadic luminance pattern (grating) when this retinal pattern was identical to it (correlated), and it enhanced perceived contrast of a postsaccadic grating when the retinal luminance pattern was inverted (anticorrelated). The difference between contrast attenuation and enhancement was stronger around the centre of gaze compared to the periphery. This study suggests that any presaccadic stimulation, such as a fixation cross, can change the processing of postsaccadic information; and this does not even require prolonged fixation durations. Therefore, it stresses the importance of reducing the number of features that could be adapted during the presaccadic fixation period. Luminance especially seems to be a feature that puts strong and persistent afterimages onto the postsaccadic percept; this can be avoided, when one uses stimuli that are isoluminant towards the background, such as the fixation stimuli we used in the other three studies.

Study IV together with findings by Samonds et al. (2018) hints at an important consideration to make when asking for why and of what amplitude humans and other animals make saccades. Samonds and colleagues (2018) found that saccade amplitudes of many species including mice and humans could be predicted by calculating the necessary distance to maximally decorrelate two circular regions on a natural-scene image. Those regions represented the pre- and the postsaccadic position of a receptive field of a visual neuron that quickly adapts to an unchanging input. The rationale was that a full decorrelation between pre- and postsaccadic inputs maximises the neuron's response and on average the response of a neuronal population. The fact that some species typically make larger saccades (mice) or smaller saccades (humans) could be reliably determined given their average receptive field sizes. Interestingly, since mice do not have a fovea but a rather uniform resolution across their visual field (Dräger & Olsen, 1981; Jeon et al., 1998), decorrelating pre- and postsaccadic information and hence counteracting adaptational effects might be one of the major reasons why mice make saccades; and this function seems to have remained in humans as well.

We could confirm one major assumption Samonds et al. (2018) made: that rapid neuronal adaptation would survive a saccade at all and affect postsaccadic perception depending on the degree of correlation between pre- and postsaccadic stimulation. This indicates that the aim of decorrelating pre- and postsaccadic inputs, achieved by executing appropriately large saccades, could indeed be relevant for humans. However, the relationship between receptive field sizes and saccade amplitude may only apply to gaze behaviour in passive viewing (Samonds et al., 2018) such that this purpose of scaling saccade amplitudes is overwritten by superior goals such as foveating a relevant target. It may still be conceivable that even with a particular saccade target location (like in transsaccadic-perception paradigms) saccades aim to not directly re-occupy a retinal location that might suffer from correlated presaccadic stimulation for instance by undershooting the target slightly.

4.3 Transsaccadic segregation resulting from perceptual experience

The results of the second and third study both suggest that the ability to segregate pre- and postsaccadic information is adaptive to transsaccadic experience. With transsaccadic experience I refer to the processing of visual information from the time around saccades. Specifically, saccades should induce a reoccurring pattern of perceptual experience; an aspect that has been more generally referred to as sensorimotor contingencies (O'Regan & Noë, 2001). In the following, I will elaborate on the nature of transsaccadic contingencies in light of Studies II and III, and on the implications following from the learning of transsaccadic experiences — i.e., the perceptual consequences of transsaccadic expectations.

In Study II, children's saccade metrics revealed that they might experience larger and more variable saccade landing errors than adults. This may imply that the visual system of children uses this perceptual experience to decide whether a postsaccadic retinal error could be self-induced or due to an externally caused displacement (Niemeier et al., 2003). For children, larger and more variable retinal errors should be expected to be self-induced than for adults. This should then lead children be less likely to detect a range of externally caused displacements as a larger proportion should be assigned to be self-induced errors. Indeed, we found stronger SSD for children — i.e., a reduced tendency to segregate transsaccadic location information. While saccade landing variability seems to predict saccadic segregation behaviour well (Niemeier et al., 2003, 2007), it might still be that other differences between children and adults caused the differences in segregation performance.

One factor may be an impaired ability in children to recruit sufficient attentional resources for higher task demands (Karatekin, 2004). However, several factors suggest that attention spent on the task was high for children. First, the cartoon animals we used as saccade targets are likely to have helped children focus on the saccade task: Irving et al. (2011) showed how saccade metrics related to attention are affected by stimulus type (sim-

ple dot versus cartoon animal) across an age range between 3 and 30 years. The authors found that the stimulus type affected saccades of children (3 to 12 years); especially the rate of initiating a saccade upon target presentation at all or in the correct direction (higher with cartoons), and their reaction time i.e., their saccade latencies (lower with cartoons). Second, we found saccade latencies (Figure 4B) to be lower than to be expected for this age range with simple dot targets (ca. 300 ms estimated from Irving et al., 2011)[2] and in the range of saccade latencies to be expected for this age group with animal cartoons as targets (ca. 200 ms estimated from Irving et al., 2011).

Even if the remaining difference in attention allocation between children and adults would have been responsible for the effect in SSD, then this should have affected blank- and no-blank conditions similarly, but we found a larger difference between blanking conditions for children compared to adults indicating that there was an additional factor involved. Bruno et al. (2006) also found stronger saccadic suppression of contrast sensitivity (SSCS) in adolescents (12 to 14 years) compared to adults (21 to 31 years) even though saccade latencies did not differ between groups (as a marker of attention). In addition, perisaccadic sensitivity was similarly high for both age groups when there was no luminance information to be suppressed (with targets that did not carry luminance information: equiluminant gratings modulated in chromaticity). As outlined in the introduction (section 2.2), SSCS and SSD are highly related phenomena; it is unlikely that there is stronger SSD in children because of attentional deficits but that there is also stronger SSCS not caused by attentional deficits. Also stronger SSCS in children and adolescents compared to adults has been inferred to be due to differences in saccadic uncertainty, partly because lower-level contributors to SSCS (e.g., masking) should be no different from those in adults by the age of 2 years (Morrone & Burr, 1986; Skrandies, 1987; as cited in Bruno et al., 2006). To summarise, it seems to be the most conclusive explanation that children show stronger SSD and a larger blanking effect than adults due to higher saccadic uncertainty. This uncertainty may emerge from the perceptual experience of high variability in object locations between pre- and postsaccadic vision.

Transsaccadic experience should not solely concern target location but should be characterised differently for every visual feature dimension. This is because a position change on the retina implies changes in information processing (for a review see Stewart et al., 2020). For example, Study III revealed that shape appears differently between presaccadic peripheral and postsaccadic foveal vision such that shapes become less circular (more triangular) towards the fovea across saccades. Here the question arises as to why shapes are perceived to be more circular in presaccadic vision in the periphery. Essential to the answer of this question might be determining how the human brain determines shape at all. Individual spatial elements such as lines or corners (signalled from V1) are supposedly grouped together to form a shape in higher-level object-processing areas such as the lateral occipital complex (for a review see Grill-Spector et al., 2001); this grouping information

[2]For a comparison to additional studies, see Table A4 in Publications - Study II (Appendix).

is fed back to lower-level processing areas such as V1 which causes a reduction in activity where neurons process input in accordance with the shape (e.g. local lines), and an enhancement in activity where low-level shape information is missing but the feedback shape information defines something to be there (Kok & de Lange, 2014). For instance, contour information of a shape may be missing due to partial occlusion of an object; nevertheless, simple geometrical shape contours can be perceived continuously such as famously illustrated in "Kanizsa" figures (Kanizsa, 1976).

Low-level contour information might not only be unavailable to V1 due to occlusion but also due to lower resolution and spatial summation with increasing eccentricity from the fovea (for reviews, see Strasburger et al., 2011; Rosenholtz, 2016). Illustrations of the approximated low-level information available for shape can be found in the work by Valsecchi et al. (2018), who manipulated overlapping geometric shape stimuli using an image-manipulation algorithm that was designed to simulate all aspects of low-level peripheral processing (Eidolon factory, Koenderink et al., 2017). Valsecchi et al. (2018) also investigated perception of such irregular shapes and found that they are perceived as less irregular when they are presented to the periphery compared to the fovea. This suggests that, similar to Kanizsa-shapes, the brain also constructs simple geometric shapes from fragmentary peripheral information following early theories of Gestalt psychology that objects will take on a "prägnant", simple geometric shape (Koffka, 1935; for a review see Wagemans et al., 2012).

The question remains as to why a more circular shape or a circle might be the "simplest" shape in comparison to a more triangular shape or a triangle. One answer may be that, physically, circles or spheres are the more (or most) symmetrical and regular objects. It may be that not only mirror symmetry facilitates perceptual grouping of individual elements (Machilsen et al., 2009), but other symmetries (e.g. rotational symmetry) in addition. It should be considered, however, that symmetry or simplicity is an intuitive property but if one takes the stance that the visual system should adjust to perceptual experience and that also Gestalt rules might have their origin in perceptual experience (e.g., Brumswik & Kamiya, 1953; Kim et al., 2021), the more important property would be if circles were the shapes most likely encountered in everyday perception e.g., in natural scenes.

Sigman and colleagues (2001) investigated geometric regularities in natural scenes and found that edges or line segments most likely lie on a common circle (co-circularity) but that does not imply that circles are the most common shapes in natural scenes; it rather indicates a prevalence of closed smooth contours (Chow et al., 2002). After all, circular objects might induce the most coherent inputs from different viewpoints (e.g., a ball shows the same circular shape from all viewpoints). In addition, it can be assumed that the geometrical centre of an object as well as its mass centre can be estimated more accurately when abstracted to a circle (Bingham & Muchisky, 1993), which may be beneficial for behavioural interaction. Overall, there are good reasons why presaccadic peripheral perception is biased towards circularity such that smooth contours are more common in

natural scenes and that a circle is a parsimonious and useful approximation of object shape.

Taking the findings of Studies II and III together, transsaccadic experience of object location variance and deterministic shape changes seem to be learned by the visual system to guide transsaccadic segregation. The "knowledge" of regularities in transsaccadic perception may be attributed to transsaccadic expectations, based on which the visual system can make case-specific predictions on the properties of postsaccadic information triggered by the current presaccadic input. Transsaccadic expectations should entail knowledge on the typical size and direction of a transsaccadic feature change. While other studies showed that different sizes of target displacements lead to more or less segregation dependent on displacement direction (orthogonal vs. parallel to saccade, Niemeier et al., 2003, 2007; Wexler & Collins, 2014; Atsma et al., 2016), Study III is the first study to indicate such a directional aspect for a property that is not target location: shapes typically become less circular (or smooth) across saccades and hence changes that increase circularity were more likely to be detected. It can be assumed that in general transsaccadic expectations lead to better transsaccadic segregation when the stimulus properties change in a direction opposite to the expected. Those expectations should theoretically be acquired from everyday perception and generalise across many stimulus types (e.g., artificial or natural); but their effects on perception are potentially even stronger for more naturalistic stimuli than those used in Study III.

Lastly, following this theory of transsaccadic expectations, intrasaccadic displacement perception only within the axis parallel to a saccade should also reveal a direction bias: transsaccadic experience for object location may be based on the distance between the target object and the current centre of gaze before and after the saccade, and pre- and postsaccadic distances should more often have the same sign (both to the left, or both to the right), because saccade undershoots are more likely than overshoots (e.g., van Opstal & van Gisbergen, 1989). It follows, that opposite signs (e.g., presaccadic distance to the right and postsaccadic distance to the left) such as those induced by inward stimulus displacements, should contradict transsaccadic expectations and be perceived more often. Such a bias can be found in the data shown by Wexler and Collins (2014), but was not discussed, and also not observed in any earlier studies (e.g., Bridgeman et al., 1975) or in Study II, and the opposite relationship was found in the studies by McConkie and Currie (1996) and Souto et al. (2016). There is a substantial interaction problem between the direction and the magnitude of discrepancy in intrasaccadic displacement studies: outwards displacements together with saccade undershoots lead to a larger postsaccadic discrepancy between landing- and stimulus position (postsaccadic retinal errors). This could outweigh a change signal due to unusual transsaccadic change direction caused by inwards displacements (which should mostly produce perfect target landings postsaccadically) or, be even weighted more heavily (McConkie & Currie, 1996).

4.4 The dichotomy of integration and segregation

Here I elaborate on an essential question that is on the basis of this dissertation: whether transsaccadic integration and segregation are the two opposing outcomes of the same mechanism such that more integration automatically leads to less segregation and vice versa.

There seems to be a consensus in the literature that a reduced discrepancy between cues facilitates integration and in turn, that increased discrepancy impedes it (for a review see Ernst & Bülthoff, 2004). Fittingly, increased discrepancy between pre- and postsaccadic signals seems to facilitate segregation such that for instance larger displacements are more easily detected (e.g., Bridgeman et al., 1975). A model on transsaccadic perception of displacement states that the final transsaccadic percept is a combination of an integrated and a segregated percept each weighted by factors determining object continuity (Atsma et al., 2016). This model might imply that more segregation automatically results in less integration and vice versa. In other words, the more likely a participant is to detect an intrasaccadic change, the smaller will be a perceptual precision benefit from integration. To systematically address the question, the degree to that segregation is improved by some intrasaccadic change should be compared to the degree of impairment of transsaccadic integration.

Demeyer and colleagues (2010b) investigated transsaccadic perception of shape (more or less circular ellipses and squares) with or without a postsaccadic blank, or a postsaccadic mask stimulus intervening. The participants' task was to report whether the pre- and postsaccadic shapes were one and the same or two separate objects (main experiment, part 1), or to judge the shape of the postsaccadic stimulus on a scale (main experiment, part 2). Proportion separate-objects reports was low with small shape discrepancies between pre- and postsaccadic stimuli and quickly reached ceiling with large shape discrepancies or a postsaccadic mask or blank. Importantly, the authors found a reduced influence of the presaccadic information on the postsaccadic percept when a postsaccadic blank intervened, potentially indicating that integration is impaired with increased object discontinuity (at least mean averaging). However, the authors mention the possibility that the memory trace (visual analogue) of the presaccadic information could have slightly decayed during the blank interval, which might cause the reduced influence of this information.[3] Interestingly, the precision of shape judgements was no different between conditions, potentially indicating that transsaccadic integration was not impaired given the strong object discontinuities the authors applied. Nevertheless, it is unknown whether participants integrated pre- and postsaccadic information at all in any of those conditions because a precision enhancement with respect to pre- and postsaccadic perception only was not tested.

[3] This might rather imply a lower weighting of the (now less reliable) presaccadic information instead of less optimal integration.

When we tested transsaccadic integration of numerosity information (Study I), even in the fourth experiment in which we implemented strong changes in luminance across saccades, participants integrated information close to predicted. Moreover, in a questionnaire completed after the experiment, almost all participants reported to have detected a change in at least one trial. While the proportion of detected changes might still be very low, it could also be that changes can be detected and simultaneously pre- and postsaccadic information can be integrated to serve the task and a more accurate estimate.

Further doubts that facilitated segregation implies impaired integration may arise considering the need of attention for both percepts. It has been shown that optimality of integration is impaired when a visual distractor is presented, especially right before saccade onset (Stewart & Schütz, 2018a); and that presaccadic attention located away from the presaccadic target location (as inferred to follow from saccadic adaptation) reduces the integration of the presaccadic target information into the postsaccadic percept (Van der Stigchel et al., 2020). In turn, it is hard to believe that such attentional distraction or delocalisation would facilitate segregation performance. In fact, it is a well-established finding that the detection of stimulus changes requires attention (e.g., Henderson & Hollingworth, 1999; O'Regan et al., 1999). Another indication that transsaccadic segregation also depletes attentional resources comes from studies showing that the recognition of a postsaccadic letter is impaired if large intrasaccadic feature changes or a postsaccadic blank were applied to the object containing the letter (Poth et al., 2015; Poth & Schneider, 2016). To summarise, a lack of attention should impair both integration and segregation of transsaccadic information. This may suggest that both perceptual outcomes rely on the same resources potentially being the basis of the same mechanism (that is either fully active or not) but not that no occurrence of one automatically implies the occurrence of the other.

In conclusion, there is no direct evidence against a causal inference mechanism that weights integration or segregation based on perceptual evidence for or against external stability (a common cause) as suggested by Atsma et al. (2016). This implies that once this process is started, integration and segregation are indeed opposing outcomes of one mechanism. However, no integration should not automatically lead to segregation or vice versa as a lack of attentional resources would impair both, meaning that the inference process would be impaired as a whole. What will be perceived when information is neither segregated nor integrated would be an interesting question as well. It might be a percept of the current (postsaccadic) information only: not influenced by the presaccadic information (no integration) and not compared to it (no segregation).

4.5 Future perspectives

While this dissertation contributes to the understanding of transsaccadic perception it also leads to new questions providing a promising avenue for future research. A first ques-

tion that still awaits systematic investigation follows directly from the previous section 4.4. As suggested by the intriguing finding of Study I that close-to-optimal transsaccadic integration can be observed for numerosity estimation even when global luminance changes intervened: transsaccadic integration may occur in conditions that typically foster transsaccadic segregation. It may be, that the detection of a change in some task-irrelevant feature can be detected and task relevant information can be integrated in parallel and hence that optimal integration does not preclude segregation and vice versa. This possibility should be addressed by testing the necessary evidence for optimal integration such as reliability enhancement under conditions that evidently lead to intrasaccadic change detection.

Results from Study II and III suggest that perceptual experiences probably acquired over a longer period in everyday perception affect transsaccadic perception as measured under laboratory settings. One such long-term transsaccadic expectation may be that the shape of objects becomes less circular across saccades. For similar shape stimuli as we used in Study III, other studies could show that artificial transsaccadic contingencies could be learned within about half an hour of learning and could alter presaccadic target appearance (Herwig et al., 2015; Paeye et al., 2018). Interestingly, such short-term transsaccadic expectations seem to be more general visual-field expectations because learning associations between objects shifting between the periphery and fovea without saccades (stimulus moves and not the eye) seems to work as well (Paeye et al., 2018; but see Cox et al., 2005; Herwig & Schneider, 2014; Valsecchi & Gegenfurtner, 2016). It may be interesting to investigate potential differences or similarities between long-term and short-term expectations. For instance, whether a (long-term) bias for detecting circularity-increase changes would show when a stimulus simply changed position on the retina without a saccadic eye movement. Additionally, since only the effect on presaccadic appearance has been tested for short-term expectations, it is clearly interesting to test the effect on transsaccadic segregation performance as well; biases for detecting a feature change opposite to the one learned should emerge. Another interesting question would be how long-term expectations influence the acquisition of short-term expectations. For instance it may be that a transsaccadic change that is more visible than another either facilitates learning in its change direction due to larger prediction errors (Rescorla & Wagner, 1972) or dampens its rate (Köller et al., 2020; but see Weiß et al., 2014; Paeye et al., 2018, Experiment 2) due to increased evidence against a common cause in causal inference (Körding et al., 2007; Atsma et al., 2016). However, it may be conceivable that expectations serve to inform causal inference processes but are not also the result of it. They might be acquired automatically without consideration of the underlying cause of events.

While it is interesting to investigate the relationship between long- and short-term expectations, it is certainly also crucial for the field of transsaccadic perception to characterise the natural (long-term) expectations for all feature dimensions. For example, appearance of spatial frequency (Davis et al., 1987), or motion speed (Campbell & Maffei, 1979, 1981)

differs across the visual field and hence change detection biases against the typically experienced change direction across saccades should be found. In addition, it may be that transsaccadic expectations are the only mediator behind transsaccadic segregation effects. For instance even a blanking effect could be explained by a strong contradiction of the expectation to find the saccade target somewhere within an elliptic postsaccadic window (Wexler & Collins, 2014). Overall, this line of research potentially provides further evidence for a comprehensive theory of transsaccadic segregation that is based on perceptual experience.

Finally, an important question following from Study IV that found rapid retinotopic adaptation effects that persisted across saccades, is whether there is also rapid spatiotopic adaptation. Recent evidence supports the assumption that spatiotopic adaptation effects exist (T. He et al., 2018; Ge et al., 2021) but not for all kinds of features (e.g., D. He et al., 2017). The minimal adaptation duration that was used to show spatiotopic adaptation effects was three seconds. It would be of high interest for one investigating transsaccadic perception, to see whether such effects can be seen after a duration equivalent to saccade latencies (about 200 to 250 ms in overlap paradigms as used in Studies I, II, III; Saslow, 1967). If this was the case, adaptation during presaccadic target observation would cause repulsive effects on the postsaccadic appearance. In fact, a small number of participants in Study III have reported a shape percept that was not amongst the shape stimuli physically presented. They reported the occasional observation of an inverted triangle with rounded corners, which could, in theory be caused by adaptation to a triangle in presaccadic vision affecting perception of a circle in postsaccadic vision. While this observation was only phenomenological and also very rare even within the two participants who reported it, it would be important to know and consider such effects for investigating transsaccadic perception. Especially when investigating transsaccadic integration because spatiotopic adaptation would affect trials where pre- and postsaccadic information is provided to the observer (integration trials) but not when only postsaccadic information is presented (foveal/postsaccadic trials).

5 Conclusions

This dissertation investigated perception across saccadic eye movements and found the following interrelations between pre- and postsaccadic information:

1. Pre- and postsaccadic information on the number of elements in a stimulus (numerosity) can be integrated across saccades. Transsaccadic numerosity perception can be closely predicted by maximum likelihood integration even when pre- and postsaccadic stimuli differ substantially in a task-irrelevant feature dimension. Therefore, transsaccadic integration appears to be a perceptual outcome resistant to larger discrepancies between pre- and postsaccadic information.

2. Segregation of pre- and postsaccadic location information and hence the ability to detect intrasaccadic displacements appears to develop from childhood to adulthood together with the ability to accurately and precisely saccade towards a target. This latter ability might be learned by the visual system and used to infer the causal relationship between pre- and postsaccadic location information.

3. Shape appears differently in presaccadic peripheral vision compared to postsaccadic foveal or parafoveal vision such that objects appear more circular before a saccade. Segregation of pre- and postsaccadic shape information is facilitated when circularity physically increases across a saccade. Typically experienced contingencies between pre- and postsaccadic vision (circularity decrease) seem to be learned by the visual system and events contradictory to these expectations (circularity increase) seem to facilitate transsaccadic segregation.

4. Presaccadic luminance stimulation adapted during brief fixation durations (0.1 to 1.7 seconds) can affect postsaccadic contrast perception and persist even longer in time. Such rapid and persistent perceptual adaptation effects should be taken into account for the investigation of transsaccadic perception.

This work helped to characterise transsaccadic integration, transsaccadic segregation, and pre- and postsaccadic perception. In addition, this work strongly supports a theoretical framework based on transsaccadic experience to account for phenomena in transsaccadic perception.

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Publications

Four manuscripts, of which each is either published in, or currently under review for publication in a pertinent, peer-reviewed journal can be found under this chapter. The order of manuscripts corresponds to the ordering of studies listed under Study summaries. Study I and Study II have been published in *Journal of Vision*. The third study has been published online in *Vision Research* and will be published as printed version in September 2021. The fourth study is under review for publication in *iScience*. A breakdown of author contributions to each manuscript can be found under Author contributions.

Study I

Numerosity estimation benefits from transsaccadic information integration

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Humans achieve a stable and homogeneous representation of their visual environment, although visual processing varies across the visual field. Here we investigated the circumstances under which peripheral and foveal information is integrated for numerosity estimation across saccades. We asked our participants to judge the number of black and white dots on a screen. Information was presented either in the periphery before a saccade, in the fovea after a saccade, or in both areas consecutively to measure transsaccadic integration. In contrast to previous findings, we found an underestimation of numerosity for foveal presentation and an overestimation for peripheral presentation. We used a maximum-likelihood model to predict accuracy and reliability in the transsaccadic condition based on peripheral and foveal values. We found near-optimal integration of peripheral and foveal information, consistently with previous findings about orientation integration. In three consecutive experiments, we disrupted object continuity between the peripheral and foveal presentations to probe the limits of transsaccadic integration. Even for global changes on our numerosity stimuli, no influence of object discontinuity was observed. Overall, our results suggest that transsaccadic integration is a robust mechanism that also works for complex visual features such as numerosity and is operative despite internal or external mismatches between foveal and peripheral information. Transsaccadic integration facilitates an accurate and reliable perception of our environment.

Introduction

The majority of the human visual field conveys information with low visual resolution. Only a relatively small central part, the fovea, provides high-resolution visual information. Our visual system uses this architecture to locate potentially relevant objects in the periphery. Subsequently, the eyes move to project relevant objects onto the fovea and gain high-resolution information. With each of these eye movements, the position and resolution of objects on the retina changes, leading to the questions of how the brain achieves perceptual stability (for reviews, see Melcher & Colby, 2008; Mathôt & Theeuwes, 2011; Higgins & Rayner, 2015) and how pre- and post-saccadic information are combined. Recently, it has been shown that presaccadic peripheral information and postsaccadic foveal information are indeed integrated (Ganmor, Landy, & Simoncelli, 2015; Wolf & Schütz, 2015). Pre- and postsaccadic information were weighted according to their relative reliability, leading to statistically optimal integration according to the maximum-likelihood principle (Ernst & Bülthoff, 2004).

Although these studies present strong evidence for transsaccadic integration of information, they do not speak to a long-standing controversy in the study of transsaccadic perception, namely the level at which information is combined across saccades. Information could be combined at an early, image-based representation (transsaccadic fusion) or at a late representation (transsaccadic memory), when more abstract information has been extracted. In the 1980s, several studies refuted transsaccadic fusion (Jonides, Irwin, & Yantis, 1982, 1983; Bridgeman & Mayer, 1983; Irwin, Yantis, & Jonides, 1983; O'Regan & Lévy-Schoen, 1983) by presenting two stimuli that would yield a gestalt when combined in rapid succession. When the stimuli were presented during a fixation, participants fused the stimuli and easily recognized the gestalt. But when the stimuli were presented with a saccade in between, participants did not recognize the gestalt, suggesting that there was no fusion. However, a recent study provided evidence for transsaccadic fusion by reducing the duration and contrast of the postsaccadic stimulus, leading to fused percepts (Paeye, Collins, & Cavanagh, 2017). On the one hand, such a transsaccadic fusion

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mechanism might be very useful to aid the transfer of information across saccades. On the other hand, an image-based fusion might lead to distortions of visual perception when peripheral and foveal representations are incommensurate, for instance due to differences in resolution and sensitivity.

One example of a miscalibration between peripheral and foveal vision that might complicate transsaccadic integration is the perception of number in dot fields. Valsecchi, Toscani, and Gegenfurtner (2013) have shown that numerosity is underestimated in the periphery when compared to the fovea. Such a miscalibration is a challenge for transsaccadic integration and has to be compensated to achieve perceptual stability. Besides this inhomogeneity across the visual field, numerosity of dot fields is also interesting for the study of transsaccadic integration because these dot fields could be integrated on two distinct levels: on an image-based representation where, for instance, contrast information about each dot is combined across saccades, or on an abstract representation where global stimulus properties such as number are already extracted. Such an abstract representation should exist, since it has been shown that numerosity is a primary visual attribute that is analyzed independently from other visual attributes such as texture density (Burr & Ross, 2008; Anobile, Cicchini, & Burr, 2013; Cicchini, Anobile, & Burr, 2016). Interestingly, it has been suggested that the balance between numerosity and texture density differs between foveal and peripheral vision, due to differences in crowding (Anobile, Turi, Cicchini, & Burr, 2015). This could mean that peripheral information about dot fields is dominated by texture density and foveal information by numerosity. These complexities of numerosity perception make it questionable whether the visual system is nevertheless able to integrate information from the periphery and the fovea. Here we want to address this question and adapt the method of Wolf and Schütz (2015) to numerosity judgments.

In the first experiment, we compared perceptual performance in three conditions. In the foveal condition, information was presented to the participants solely in the fovea after a saccade. In the peripheral condition, as opposed to the foveal condition, solely peripheral information was shown before a saccade. To test whether there was an improvement in performance and compare this to the benchmark of maximum-likelihood integration (Ernst & Bülthoff, 2004), foveal and peripheral information was provided in the integration condition. In three further experiments, we studied which divergence of peripheral and foveal information can be tolerated by transsaccadic integration. This is an interesting question because it might help to elucidate which type of information—image based or abstract—is retained across a saccade and on which level transsaccadic integration operates. In Experiment 2, only local stimulus features, such as location and color of individual dots, were changed during the saccade. Previous research has shown that these local features are not necessarily represented and that local changes might be missed, especially under conditions of motion (Saiki & Holcombe, 2012). In Experiment 3, global stimulus features, such as the overall color of the dot field, were also changed during the saccade. Experiment 4 explicitly tested transsaccadic integration, as in Experiment 1, for the most extreme case of object discontinuity applied here.

Methods

Participants

Thirty-nine participants who were unaware of the purpose of our experiments and author CH participated in the first experiment (29 women, 11 men; mean age = 23 years, range = 19–33; all right-handed). We had to exclude the data for five participants because there were not enough valid trials, and of another participant because of a response bias leading to a strong deviation in the point of subjective equality. For all following experiments, we reinvited participants based on their performance in the first experiment. As we wanted to measure how disrupting object continuity impairs transsaccadic integration, reinvited participants' data should indicate transsaccadic integration benefits in the form of showing better performance in the integration condition than in the single conditions. Thirteen of the reinvited participants (10 women, three men; mean age = 23 years) took part in the second experiment. Another 13 of the reinvited participants (nine women, four men; mean age = 22 years) took part in the third experiment. For the fourth experiment, 12 of the participants from Experiments 2 and 3 were tested (nine women, three men; mean age = 22 years). One of them showed an extreme decrease in performance compared to all other participants and was excluded from analysis. Observers were students of Marburg University and were reimbursed for participation. Experiments were in accordance with the principles of the Declaration of Helsinki and approved by the local ethics committee of the psychology department at Marburg University (proposal number 2015-35k). All observers gave informed consent and had normal or corrected-to-normal vision.

Stimuli

Fixation stimuli were of a design that has been demonstrated by Thaler, Schütz, Goodale, & Gegenfurtner (2013) to be especially suitable for maintaining fixation on a screen. This combination of a bull's-eye and crosshair had a diameter of 0.5° of visual angle and was used for fixation at the beginning of a trial as well as a target stimulus for saccade initiation in foveal trials. The color of the fixation stimulus was chosen randomly out of an array of colors of low contrast to avoid aftereffects. The color of the target stimulus was black to reduce variability of saccade latencies. Numerosity stimuli were circular windows filled with black and/or white dots on a gray background. The size of the circular window was kept constant, with a radius of 2.6° of visual angle. Dot positions were assigned randomly, with the constraint of having a minimal center-to-center distance of 0.15°. With a radius of 0.05°, the dots did not overlap. Depending on the trial, between 20 and 80 dots were presented. This corresponds to a dot density of 0.98–3.91 dots/$^{\circ 2}$. Masking stimuli in all experiments were spirals within a circular window with the same size and positions as the numerosity stimuli. The composing colors of the spirals were increments of black and white.

Equipment

Stimuli were presented on a 91- × 51-cm back-projection setup with a PROPixx projector (VPixx Technologies, Saint-Bruno, Canada) and screen from Stewart Filmscreen (Torrance, CA). The screen had a resolution of 1,920 × 1,080 and a refresh rate of 120 Hz, with a viewing distance of 106 cm. Background luminance was 92 cd/m^2 and the screen was calibrated to ensure a linear gamma correction. Luminance was at 3.3 cd/m^2 for black pixels and 187 cd/m^2 for white pixels. Eye movements were recorded with an EyeLink 1000 (SR Research Ltd., Ontario, Canada) with a sampling rate of 1000 Hz. Experimental software was written in MATLAB using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Participants responded using a standard keyboard.

Procedure

The aim of Experiment 1 was to measure perceptual-discrimination performance for numerosity when different sources of visual information were provided. In integration trials (Figure 1), both sources of numerosity information—peripheral (before a saccade) and foveal (after a saccade)—were provided. Peripheral numerosity information was omitted for foveal trials. Therefore, the saccade target consisted of a black target stimulus which was replaced by a numerosity stimulus when a saccade was initiated. Conversely, the foveal numerosity information was dismissed for peripheral trials such that the numerosity stimulus was replaced by a black target stimulus as soon as the participant initiated a saccade.

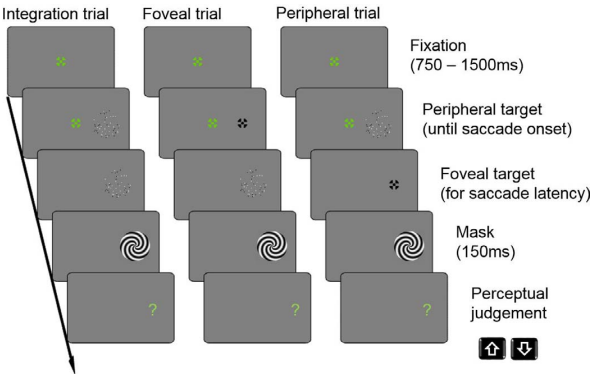

Figure 1. Trial procedure. Experiments 1 and 4 contained integration trials, foveal trials, and peripheral trials. In Experiments 2 and 3, only integration trials were tested. Every trial started with a fixation at the center of the screen. After a randomized interval, a saccade target appeared on the left or right at 12° eccentricity. The foveal target replaced this peripheral target as soon as a saccade was detected. In foveal trials, the peripheral target contained no numerosity information, whereas in peripheral trials, the foveal target contained no numerosity information. In integration trials, participants gained numerosity information from both parts of the visual field. A spiral mask appeared after a duration equal to the saccade latency beforehand, to limit the processing duration of the foveal target. After 150 ms, a question mark appeared to initiate the response of a key press of the up or down arrow on the keyboard.

In all trials, participants had to indicate whether the perceived number of dots was below or above the perceived mean numerosity of all previously presented stimuli in the experiment. A fixation stimulus at the screen center prompted participants to start the trial by fixating it and pressing the space bar simultaneously. After a random time between 0.75 and 1.5 s, a target appeared 12° left or right of the screen center. The fixation stimulus was removed after an additional 200 ms (overlap paradigm). Targets switched as soon as the EyeLink detected that the eye exceeded 1.6° with respect to the screen center. This guaranteed that the target was switched during the saccade, when vision is suppressed (for a review, see Ibbotson & Krekelberg, 2011).

A black-and-white spiral replaced the foveal target after its presentation duration to prevent any further visual processing of the numerosity stimulus. The mask was present for 150 ms. At the end of each trial, a question mark appeared at the target location to signal the participant that a response should be given. Participants could press either the up arrow key to indicate that the perceived numerosity was above the mean numerosity or the down arrow key to indicate that it was below the mean numerosity.

In every trial, the foveal target was displayed for the duration of the saccade latency of the participant of the specific trial. Thus, it was assured that participants saw the foveal target for the same duration as they saw the peripheral target. For instance, if it took 200 ms from target onset to target switch, the foveal target was presented for 200 ms as well. This guaranteed that observers were provided with roughly the same amount of peripheral and foveal information within each trial. To increase the likelihood that observers also had approximately the same viewing time across trials, they received feedback when the saccadic reaction time was too fast or too slow (target switch below 157.5 ms or above 257.5 ms). In these cases, a high or a low beeping sound was played but no visual feedback about the performance was provided. Observers were told to keep their eye-movement latency within the given time window. For the first 10 trials in each experiment, the experimenter remained with the participant to give advice and answer upcoming questions regarding the task. These 10 training trials in an experiment were omitted from analysis. At the end of Experiments 2, 3, and 4, questionnaires were filled out by the participants to reveal whether a change during a saccade reached conscious experience.

Design

Experiment 1: Test for numerosity integration

In the first experiment, we measured transsaccadic integration of numerosity stimuli and compared perceptual performance to maximum-likelihood estimation. Integration and single trials (foveal or peripheral information only) were interleaved and pseudorandomized. The number of dots presented varied from 20 to 80 in eight steps (20, 30, 40, 44, 50, 56, 60, 70, and 80). Mean numerosity of the stimuli presented was 50 for all experiments. Psychometric functions per participant and conditions were sampled with nine data points based on at least an average of 10 observations. Each participant completed at least 486 trials in 45 min. Participants who successfully completed Experiment 1 and showed a better performance for integration trials than for single trials (see Results) could participate in Experiments 2, 3, and 4.

Experiment 2: Local disruption of object continuity

In Experiment 2 we studied how local changes in low-level stimulus properties affect integration performance. In the baseline condition, 50% of the dots were black and the other 50% white, and the numerosity stimulus stayed the same throughout the trial. In a comparison condition, the colors of the peripheral stimulus got swapped in the fovea, meaning that black dots turned white and white dots turned black. Please note that this manipulation affects only the local color of individual dots, not the summary statistics of the whole dot field. The same scheme was used for two additional conditions in which the proportion of black and white dots was 60%/40%. Here again, one condition involved no change between periphery and fovea and the other involved a color change in the fovea. To test for position change as well, one condition for the 50%/50% black and white stimuli involved a position change of the dots in the fovea. All five conditions were interleaved, and the experiment took around 90 min to complete. Participants completed at least 720 trials.

Experiment 3: Global disruption of object continuity

In this experiment, we made the changes between periphery and fovea more salient, such that they also affected the summary statistics of the dot field. Therefore, we used highly unbalanced proportions between black and white dots, namely 80%/20% and 100%/0%. The 50%/50% condition was additionally included for comparison. For all proportions of black and white, one condition included no change during the trial and another included a change of color during the saccade. Experiment 3 contained 864 trials and lasted for approximately 1 hr 45 min.

Experiment 4: Explicit test for integration in the 100%/0% condition

The purpose of this experiment was to test more explicitly whether participants still integrated peripheral and foveal numerosity information in the 100%/0% color-change condition. In this condition, object continuity was disturbed the most among our manipulations: All dots were black in the periphery and white in the fovea, or vice versa. As in our first experiment, we used single trials (peripheral and foveal trials) and integration trials to compare observed to predicted integration performance. Half of the integration trials contained no change in the numerosity stimulus; the other half contained a color change of the dots during the saccadic eye movement.

The experiment contained 576 trials and lasted approximately 1 hr.

Data and eye-movement analysis

Saccade onsets were detected offline using the EyeLink 1000 algorithm. Saccade latencies were defined as the first saccadic frame with respect to target onset. To keep peripheral and foveal viewing time constant, trials with saccade latencies shorter than 100 ms or longer than 400 ms were excluded from further analysis. We excluded trials in which saccadic end points deviated from the target center by more than 2.5° of visual angle. This ensured that the target was fixated after the saccade and until the target disappeared. Taking together excluded trials for saccade latency and saccade end point, participants' mean number of outliers was 8.5% ± 9.0% (range = 1.6%–49.1%) of trials. In Experiment 1 we excluded five participants who had too many invalid trials, such that the mean number of data points per fit of a psychometric function was less than 10. One participant was excluded for being more than 30% away from the true mean numerosity estimate, such that a sufficiently valid fit of a psychometric function could not be guaranteed.

Perceptual choices were converted into proportion of up-arrow responses for every stimulus numerosity, and a cumulative Gaussian was fitted to the data using psignifit 4.0 (Schütt, Harmeling, Macke, & Wichmann, 2015). The point of subjective equality (PSE) was estimated as the numerosity value corresponding to 50% up-arrow responses. Just-noticeable differences (JNDs) were defined as the standard deviation of the cumulative Gaussian. To test whether perceptual integration of numerosity is optimal according to the maximum-likelihood estimation model (for a review, see Ernst & Bülthoff, 2004), predicted JNDs for integration were calculated using

$$JND_{int\_pred} = \sqrt{\frac{1}{rel_{int\_pred}}}. \quad (1)$$

The predicted reliability of the integrated percept rel_{int_pred} should be the sum of the individual reliabilities for foveal and peripheral presentation, if independence between cues is given:

$$rel_{int\_pred} = rel_{per} + rel_{fov}. \quad (2)$$

Reliabilities can be calculated given the JND for a participant and condition:

$$rel = \frac{1}{JND^2}. \quad (3)$$

With the reliabilities at hand, the optimal peripheral weighting can be calculated by

$$w_{per} = \frac{rel_{per}}{rel_{per} + rel_{fov}}. \quad (4)$$

Results were compared using one-way repeated-measures ANOVAs and post hoc t tests. If not noted otherwise, all t tests were two-tailed and p values were compared against a Bonferroni-corrected α of 0.05.

An important prerequisite for being able to compare performance in peripheral, foveal, and integration conditions in Experiments 1 and 4 is similar saccade latencies, because presentation durations were locked to saccade onsets. In Experiment 1 we found that mean saccade latencies were slightly longer for the foveal condition (219.63 ± 30.89 ms) compared to the peripheral (202 ± 25.37 ms), $t(33) = 5.66$, $p < 0.001$, and integration conditions, (203.05 ± 26.11 ms), $t(33) = 5.78$, $p < 0.001$. The same applies for Experiment 4: Foveal mean saccade latency (212.97 ± 19.45 ms) was significantly different from peripheral mean saccade latency (191.40 ± 18.05 ms), $t(10) = 4.29$, $p = 0.002$, from the integration no-change condition (189.72 ± 16.32 ms), $t(10) = 5.94$, $p < 0.001$, and from the integration with-change condition (189.19 ± 16.11 ms), $t(10) = 5.32$, $p < 0.001$. This means that the presentation time of the foveal target was on average slightly longer in the foveal condition than in the integration conditions. This might lead to an overestimation of foveal reliability, which would result in an overestimation of predicted reliability and an overestimation of foveal weights in integration conditions. However, the duration differences were only in the order of one to two monitor frames and therefore should have only small influences on perceptual performance.

Results

Experiment 1: Test for numerosity integration

The aim of the first experiment was to study whether participants used information from both parts of the visual field to estimate numerosity optimally. First, we analyzed whether participants were more accurate in integration trials, given both peripheral and foveal numerosity information, than in single trials, given foveal or peripheral information only. Accuracy is represented in the mean of the psychometric function—that is, the PSE—when more- and less-accurate responses are balanced. Second, we analyzed whether the precision of numerosity discrimination increased with combination of peripheral and foveal information. The precision is represented in the standard deviation of the psychometric function—that is, the JND. Finally, we compared the observed JNDs in the

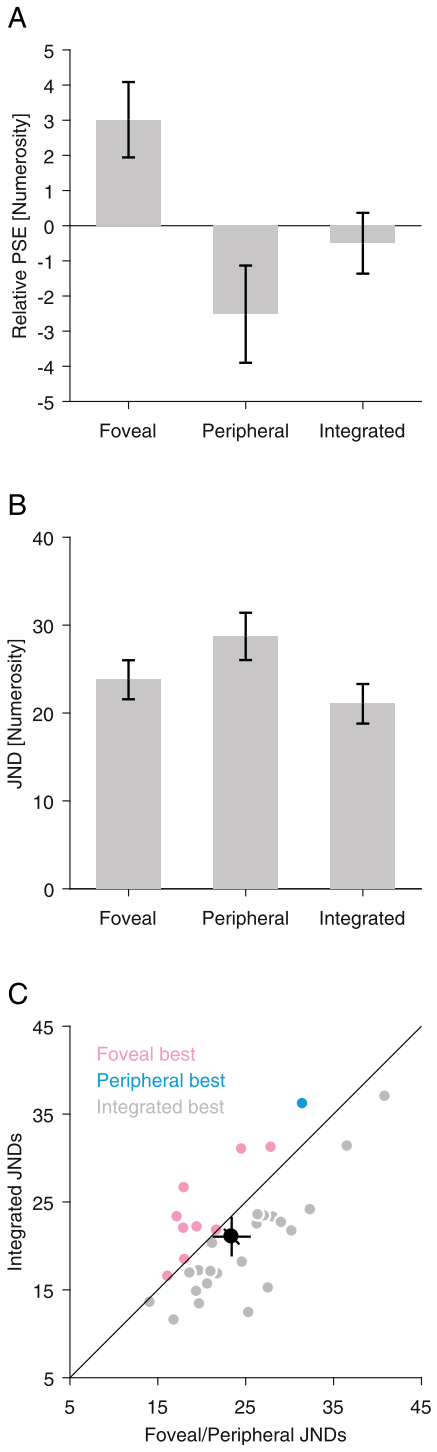

Figure 2. Relative values for point of subjective equality and values for just-noticeable difference (Experiment 1). (A) Normalized values for point of subjective equality with their 95% confidence intervals as error bars. Numerosity presented in the fovea only was slightly underestimated, whereas numerosity presented in the periphery only was slightly overestimated. Given both inputs, the point of subjective equality was closest to the true mean numerosity of the stimuli. (B) Comparison of mean values for just-noticeable difference over participants in the two single conditions and the integration condition, with 95% confidence intervals as error bars. Performance was lowest when only peripheral numerosity information was given, highest when foveal and peripheral information was provided, and in between when only foveal information was given. (C) Just-noticeable difference in integration condition as a function of the best single condition (peripheral or foveal) for every participant. Most participants were best in the integration condition (gray circles), whereas data points above the identity line were better in one of the single conditions (colored circles).

integration trials to JND values predicted by a maximum-likelihood estimation model (Ernst & Banks, 2002). These predicted JND values represent a benchmark for optimal transsaccadic information integration.

Obtaining PSEs (Figure 2A) from the psychometric functions per participant over all conditions revealed that participants in Experiment 1 rated the true mean numerosity (50) to be close to their perceived mean numerosity (49.9 ± 5.5), $t(33) = -0.10$, $p = 0.925$—not significantly different from 50). The PSE for the foveal condition was at 52.7 ± 6.8 ($M \pm SD$)—significantly different from the true mean numerosity, $t(33) = 2.29$, $p = 0.029$. This means that participants perceived a higher numerosity at the center of the distribution and therefore underestimated numerosity in the foveal condition.[1] The PSE for peripheral trials was at 47.21 ± 6.99, $t(33) = -2.39$, $p = 0.023$—significantly different from 50—showing an overestimation of numerosity in the periphery. The PSE in integration trials was not significantly different from the true mean numerosity (49.16 ± 5.46), $t(33) = -0.90$, $p = 0.375$—not significantly different from 50. Comparing the PSEs for the different conditions revealed significant differences between foveal and peripheral conditions, $t(33) = 4.85$, $p < 0.001$, and between foveal and integration conditions, $t(33) = 5.21$, $p < 0.001$. A difference close to significance was found for the peripheral and integration conditions, $t(33) = -2.01$, $p = 0.053$.

For the JNDs we found significant differences between all conditions (Figure 2B). Participants were significantly better at discriminating numerosity given foveal information only compared to peripheral information only (foveal: 23.79 ± 6.36; peripheral: 28.72 ± 7.72), $t(33) = -4.64$, $p < 0.001$. However, given both foveal and peripheral information in the integration condition (21.05 ± 6.45), participants were significantly

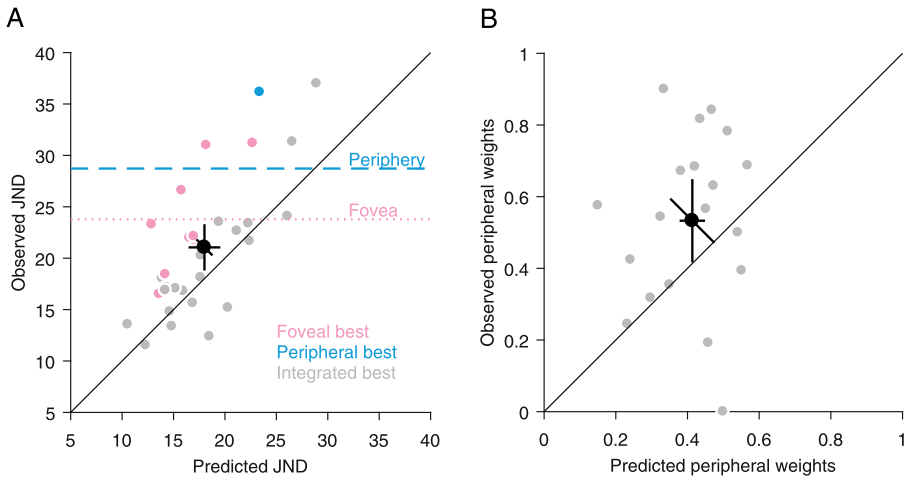

Figure 3. Optimality of integration and peripheral weighting (Experiment 1). (A) Individual data (gray and colored circles) and mean (black filled circle) comparing predicted values for just-noticeable difference (JND) for integration to observed JND values of the integration condition. Most individual data gather along the identity line indicating optimal transsaccadic integration. The mean over all participants indicates slightly worse performance than predicted, but close to optimal integration behavior. Horizontal lines depict the mean JND of the foveal and peripheral conditions. Both are above the mean JND of the integration condition. (B) Comparison of predicted peripheral weights and observed peripheral weights based on individual values for JND and point of subjective equality. Individual data are depicted as gray circles, and their mean as filled black circle, with error bars denoting 95% confidence intervals. The diagonal error bar marks the error of the differences between observed and predicted values, and has to be compared to the identity line (solid). Participants are shown to have relied on the peripheral information slightly more than predicted.

better than in the foveal condition, $t(33) = 3.13$, $p = 0.002$ (one-sided), and the peripheral condition, $t(33) = 7.36$, $p < 0.001$ (one-sided). Figure 2C shows the comparison of individual JND values for integration and the best of foveal or peripheral conditions. The result confirms the finding that performance was generally better in the integration condition, $t(33) = 2.71$, $p = 0.005$ (one-sided). Only 11 out of 34 participants were worse in the integration condition than in the foveal or peripheral conditions. According to the maximum-likelihood estimation model, integration should be optimal when the predicted JND from the model equals the observed JND of the participant (Equations 1 and 2). Figure 3A depicts this comparison and reveals a close-to-optimal integration for numerosity (observed JND: 21.05 ± 6.45; predicted JND: 18.01 ± 4.43), $t(33) = -3.98$, $p < 0.001$.

The differences between peripheral and foveal PSEs indicate a miscalibration of perceived numerosity across the visual field. Inappropriate weighting of miscalibrated signals could lead to a reduction in precision compared to the optimal predictions. To test whether peripheral and foveal information were appropriately weighted, we calculated the predicted peripheral weights (Equation 4) and compared them to the observed peripheral weights for the PSEs. For this comparison, we could only use data from participants whose PSE in the integration condition was in between their PSEs for the two single conditions (19 of 34 participants). Interestingly, the pattern (Figure 3B) indicated a higher weighting for peripheral information than predicted (observed: 0.53 ± 0.24; predicted: 0.41 ± 0.12), $t(18) = -2.17$, $p = 0.044$.

For our first experiment, participants accurately identified the true mean numerosity as their mean PSE (over all conditions). Even though numerosity perception differed significantly for peripheral and foveal vision, participants showed more accurate perception when both inputs were provided in the integration condition. The finding that the relation between the observed and predicted discrimination performance was close to the optimality line (Figure 3A) is additional evidence that numerosity information before and after a saccade is integrated almost optimally. Furthermore, participants' discrimination performance in the integration condition was significantly better than in their best single condition (foveal or peripheral), as shown in Figure 2C.

Experiment 2: Local disruption of object continuity

In our second experiment, we wanted to test whether integration performance is affected by disrupting object continuity. Therefore, we compared integration per-

formance from a baseline condition to that of a change condition. The first baseline condition was a replication of the integration condition of the previous experiment. The stimuli consisted of 50%/50% black and white dots, and stayed the same throughout a trial. The corresponding change conditions differed in the way that either the color of the dots was exchanged (50%/50% color-change condition) or the dot positions were changed (50%/50% position-change condition) during the saccade. To make the color changes during a saccade more salient, a 60%/40% black-and-white-dots baseline condition was introduced, accompanied by a 60%/40% color-change condition.

We first compared the PSEs between the five different conditions for integration trials (Figure 4A). Mean PSEs over all conditions were slightly above but not significantly different from the true mean numerosity (51.70 ± 5.09), $t(12) = 1.20$, $p = 0.252$—not significantly different from 50. A one-way ANOVA indicated a significant difference between the conditions, $F(4, 60) = 2.78$, $p = 0.035$. Post hoc t tests between the baseline and change condition pairings revealed that participants slightly overestimated numerosity when the positions of the dots changed during a saccade compared to the no-change condition, $t(12) = 3.04$, $p = 0.010$. The average JND across all conditions in Experiment 2 (18.11 ± 4.34) was below the averaged JND values for those participants in the single conditions of Experiment 1—foveal (22.17 ± 4.17), $t(12) = -4.07$, $p = 0.002$; peripheral (24.76 ± 5.55), $t(12) = -4.36$, $p < 0.001$—and close to the average predicted JND for those participants in Experiment 1 (16.41 ± 3.16), $t(12) = 1.80$, $p = 0.097$. The ANOVA performed on the JNDs from Experiment 2 indicated no significant effect among the five conditions, $F(4, 60) = 0.67$, $p = 0.618$. An additional Bayes-factor analysis (for a review, see Jarosz & Wiley, 2014) supports the null hypothesis moderately ($BF_{01} = 7.09$).

The results of Experiment 2 are in favor of the hypothesis that the perisaccadic stimulus changes did not affect transsaccadic integration of numerosity. The finding that the JND values do not differ significantly between the baseline and change conditions supports this conclusion. Furthermore, the JNDs in all integration conditions of Experiment 2 were below the JNDs of the single conditions of Experiment 1, suggesting that participants integrated despite the intrasaccadic changes.

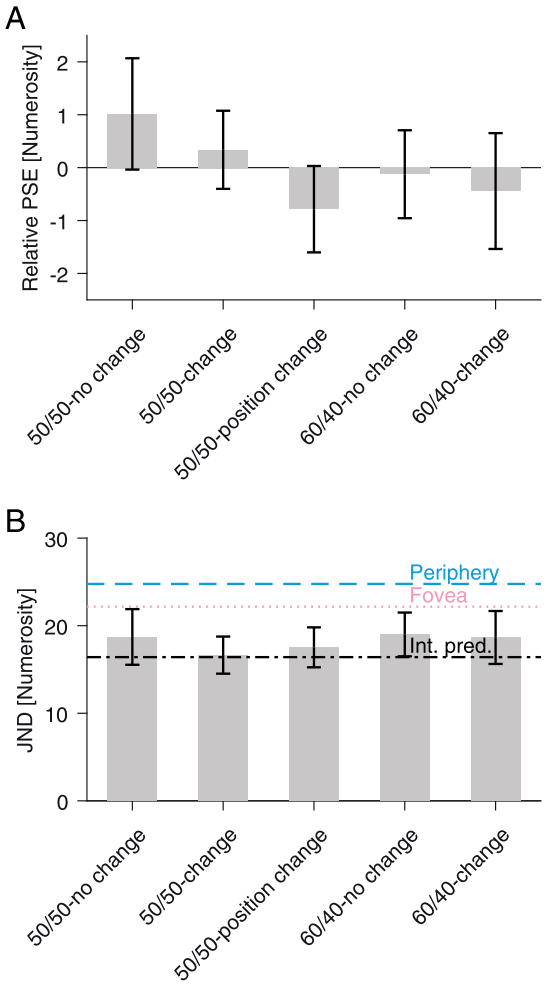

Figure 4. Values for point of subjective equality and just-noticeable difference (Experiment 2). (A) Relative values for point of subjective equality for all five conditions of the second experiment, with 95% confidence intervals as error bars. Numerosity was slightly overestimated in the 50%/50% position-change condition compared to its baseline condition (no change). (B) Mean values for just-noticeable difference over all conditions, with 95% confidence intervals as error bars. Performance did not depend on the object continuity manipulation. Horizontal lines show the mean values for just-noticeable difference for foveal, peripheral, and integration-predicted conditions from the first experiment.

Experiment 3: Global disruption of object continuity

Manipulating object continuity in the previous experiment did not affect transsaccadic integration. However, all of these manipulations affected local stimulus features, such as the color or location of individual dots, and left global stimulus features, such as the overall color, largely unaffected. Previous research has shown that changes in local features can go unnoticed easily under conditions of motion (Saiki & Holcombe, 2012) and that even the assignment of individual dots to one of two surfaces is limited (Schütz, 2012). In a similar way, such local changes

might be overlooked during saccades and therefore leave integration performance unaffected. In this experiment, we challenged transsaccadic integration with changes in global stimulus features that should not be overlooked as easily: Proportions of black and white dots were chosen to be 80%/20% for one pair of conditions (baseline and color change) and 100%/0% for another pairing. As a result, the overall brightness of the dot field changes in the color-change conditions. The 50%/50% black-and-white proportion was included again for comparison.

As in the previous experiments, we first compared the PSEs between the six different conditions for integration trials (Figure 5A). Mean PSE over all conditions was not significantly different from the true mean numerosity (51.61 ± 4.58), $t(12) = 1.27$, $p = 0.229$—not significantly different from 50. The t tests between the baseline and change pairings revealed that participants overestimated numerosity more, or deviated more strongly from the true mean numerosity, in the 100%/0% color-change condition (47.69 ± 4.28) than in the 100%/0% no-change condition (49.40 ± 5.21), $t(12) = 3.66$, $p = 0.003$. Conversely, participants underestimated numerosity slightly more in the 50%/50% change condition (55.36 ± 5.41) compared to its baseline condition (54.11 ± 6.23), $t(12) = -2.33$, $p = 0.038$.

Participants' average JND across all conditions in Experiment 3 (17.31 ± 3.92) was below the JNDs of those participants in the single conditions of Experiment 1—foveal (22.17 ± 4.40), $t(12) = -3.38$, $p = 0.006$; peripheral (24.94 ± 6.48), $t(12) = -4.14$, $p = 0.001$—and in the range of the average predicted JND of those participants in Experiment 1 (16.42 ± 3.50), $t(12) = 0.75$, $p = 0.468$. An ANOVA of the JND values from Experiment 3 indicated no significant difference overall, $F(5, 72) = 0.32$, $p = 0.898$. A subsequent Bayes-factor analysis supports the null hypothesis strongly ($BF_{01} = 15.21$).

The results of Experiment 3 show that even global disruptions of object continuity in terms of brightness or contrast polarity did not impair discrimination performance. The findings suggest that participants were still integrating peripheral and foveal information for all conditions. PSE values reveal that different proportions of black and white dots seem to influence numerosity estimation. The more unbalanced the proportions were, the more participants overestimated numerosities. However, these tendencies were not affected by color changes during a saccade.

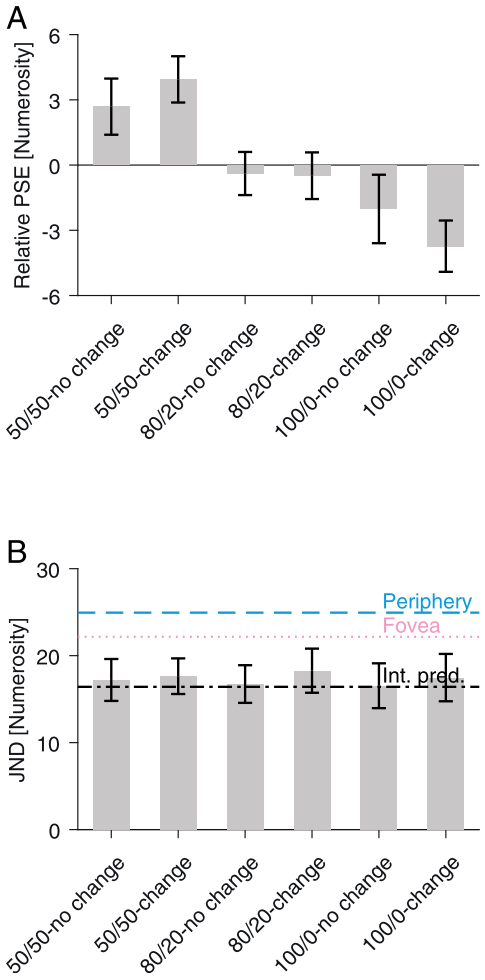

Figure 5. Values for point of subjective equality and just-noticeable difference (Experiment 3). (A) Relative mean values for point of subjective equality for all three pairs of baseline and color-change condition, with 95% confidence intervals as error bars. The degree of underestimation seems to shrink with an increased imbalance of black and white dots. (B) Mean values for just-noticeable difference over all conditions, with 95% confidence intervals as error bars. Discrimination performance was not affected by the object continuity manipulation. Horizontal lines show the mean values for just-noticeable difference for foveal, peripheral, and integration-predicted conditions from the first experiment.

Experiment 4: Explicit test for integration in the 100%/0% condition

Showing that JNDs in Experiments 2 and 3 are close to predicted JNDs in Experiment 1 and do not differ among the different conditions does not fully prove that participants actually integrated the stimuli transsaccadically. Since participants were reinvited to Experiments 2 and 3, a training effect could also be the cause of the good performance found in these experiments. To rule out this possibility, we reapplied the design of Experiment 1 to explicitly compare performance in single trials (foveal or peripheral

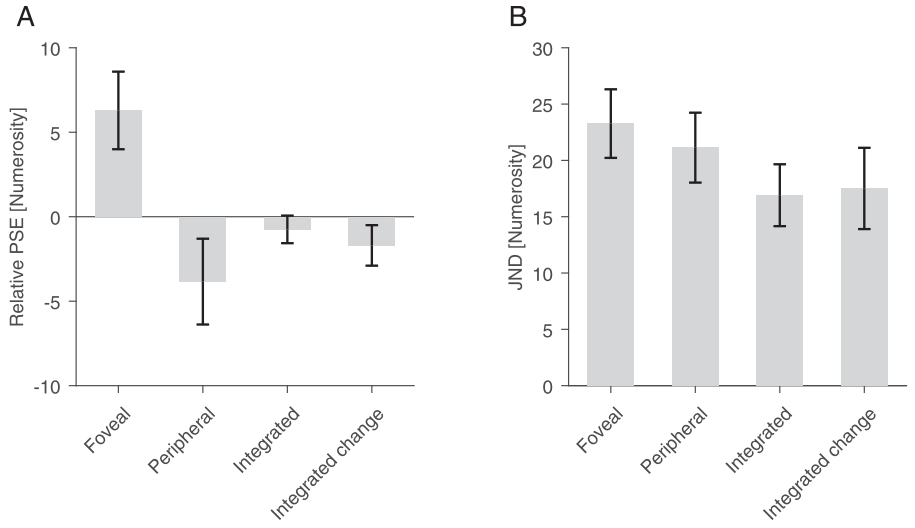

Figure 6. Values for point of subjective equality and just-noticeable difference (Experiment 4). (A) Relative mean values for point of subjective equality for the two single and the two integration conditions, with 95% confidence intervals as error bars. Numerosity was underestimated in the foveal condition, overestimated in the peripheral condition, and rather accurate in both integration conditions. (B) Mean values for just-noticeable difference over all conditions, with 95% confidence intervals as error bars. While the two single conditions and two integration conditions do not differ significantly within each pair, each condition of one pair differs significantly from each condition of the other.

information only) to performance in integration trials (both provided) for a condition with disrupted object continuity. Among the different manipulations of Experiment 2 and 3, we chose the ratio of 100%/0% black and white dots, as it implies the most salient change when the colors get swapped. The aim of Experiment 4 was to compare integration performance for these stimuli when nothing changes during the saccade, as well as when the color changes during the saccade.

Participants' averaged PSEs over all conditions were again close to the true mean numerosity (52.48 ± 4.85), $t(10) = 1.69$, $p = 0.121$—not significantly different from 50. Averaged PSEs for the four individual conditions (Figure 6A) show that numerosity was underestimated in the foveal condition (58.66 ± 6.30), $t(10) = 4.56$, $p = 0.001$—significantly different from 50—while it was rather accurate for the peripheral condition (48.53 ± 6.80), $t(10) = -0.72$, $p = 0.491$—not significantly different from 50. The average PSE was also accurate in both the integration condition without a change (51.62 ± 4.77), $t(10) = 1.13$, $p = 0.285$—not significantly different from 50—and the integration condition with color change (50.68 ± 4.27), $t(10) = 0.52$, $p = 0.612$—not significantly different from 50. Our t tests between the PSEs in all four conditions revealed a significant difference between the foveal and peripheral conditions, $t(10) = 4.87$, $p < 0.001$, and between the foveal condition and the two integration conditions: foveal and integrated, $t(10) = 6.75$, $p < 0.001$; foveal and integrated with change, $t(10) = 6.28$, $p < 0.001$. The differences between peripheral and integration conditions only reached significance for the no-change condition: peripheral and integrated, $t(10) = -2.31$, $p = 0.043$; peripheral and integrated with change, $t(10) = -1.57$, $p = 0.148$. The PSEs of the two integration conditions did not differ significantly, $t(10) = 1.41$, $p = 0.190$.

An ANOVA of the JNDs over the four conditions indicated a significant difference between them, $F(43) = 4.59$, $p = 0.008$. Subsequent t tests revealed significant differences between the foveal (23.27 ± 4.53) and integration no-change conditions (16.91 ± 4.09), $t(10) = 4.08$, $p = 0.001$ (one-sided) and between the foveal and integration with-change conditions (17.51 ± 5.37), $t(10) = 3.21$, $p = 0.005$ (one-sided). The mean JND in the peripheral condition (21.13 ± 4.62) was also significantly different from those in the integration condition without change, $t(10) = 3.28$, $p = 0.004$ (one-sided), and with change, $t(10) = 4.03$, $p = 0.001$ (one-sided). Different from the results in the first experiment, there was no difference between peripheral and foveal discrimination performance, $t(10) = 1.35$, $p = 0.208$.

Where PSEs and JNDs proved to be relatively similar for both integration conditions—JNDs of integrated versus integrated with change, $t(10) = -0.47$, $p = 0.648$—the pattern of best-of-single-conditions JNDs versus integration-condition JNDs (Figure 7A) also appears to be alike for no change and color change. Participants were better in integration condi-

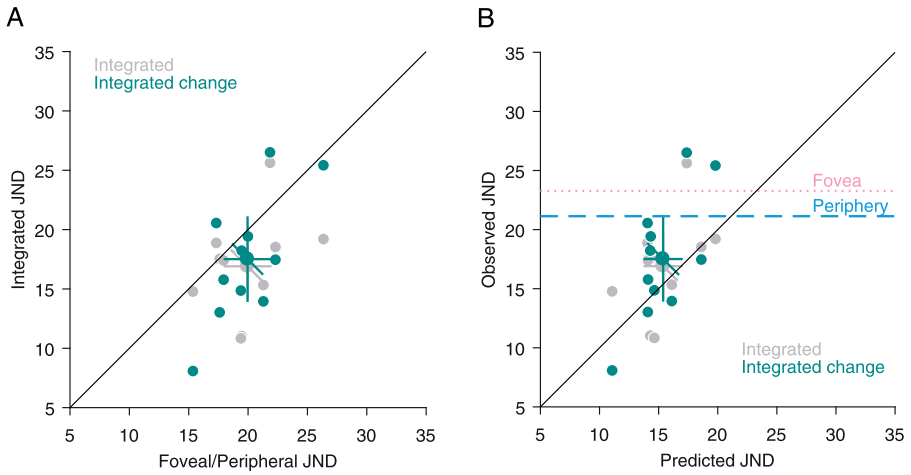

Figure 7. Optimality of integration (Experiment 4). (A) Just-noticeable differences (JNDs) in the integration condition as a function of the best single condition (peripheral or foveal) for every participant. Only three participants in the integration condition without change and two in the integration condition with color change were worse in the integration condition than in their best single condition (above the solid line). (B) Comparison of predicted JNDs with observed JNDs in each integration condition. For color change as well as for no change during a saccade, mean integration performance was close to the optimality line. The dotted line indicates the mean JND value for of the foveal condition, and the dashed line marks the mean JND of the peripheral condition.

tions than in the best single condition: best of single versus integrated, $t(10) = 2.42$, $p = 0.018$ (one-sided); best of single versus integrated with change, $t(10) = 2.08$, $p = 0.032$ (one-sided). A comparison of the JNDs predicted from the single conditions (15.37 ± 2.47) with the observed JNDs in both integration conditions revealed that, again, performance was slightly worse than predicted (Figure 7B) but close to optimality: observed versus predicted without change, $t(10) = -1.39$, $p = 0.196$; observed versus predicted with color change, $t(10) = -1.76$, $p = 0.109$.

In our last experiment, PSE values among the single and integration conditions revealed a similar pattern as we found in our first experiment. This and the reduced JNDs for both integration conditions compared to the single conditions indicate that participants integrated numerosity information across saccades even with the 100%/0% black-and-white ratio and color change between the targets.

Questionnaire

In the second, third, and fourth experiments, numerosity stimuli could change during a saccade. To evaluate whether participants consciously perceived such a change, they were asked to fill in a questionnaire after each experiment and say whether they perceived a change within the numerosity stimulus during a trial. In Experiment 2, none of the 13 participants reported such a change. In Experiment 3, eight out of 13 participants perceived a change within a trial. In Experiment 4, 10 of the 12 participants reported having seen a color change.

Discussion

Near-optimal integration of pre- and postsaccadic information has been shown previously for low-level stimuli such as spatial orientation (Ganmor et al., 2015; Wolf & Schütz, 2015). Here we show that near-optimal integration of peripheral and foveal input can be achieved as well for a high-level visual feature: numerosity. In Experiments 1 and 4, the integrated percept was more accurate despite different biases of peripheral and foveal perception. Furthermore, the integrated percept was more precise than the peripheral and foveal percepts alone and only slightly worse than the one predicted by maximum-likelihood estimation. Experiments 2, 3, and 4 showed in addition that local and global changes in low-level stimulus properties, such as the location of individual dots in the dot field or the color of the whole dot field, did not impair transsaccadic integration.

Calibration and integration of perceived numerosity across the visual field

Optimal transsaccadic integration of numerosity is challenging, since numerosity perception differs signif-

icantly in the parts of the visual field (Valsecchi et al., 2013; Anobile et al., 2015). For example, Valsecchi et al. (2013) have shown that numerosity is underestimated in the periphery when a peripheral stimulus is directly compared to a stimulus in the fovea. In contrast, in our Experiments 1 and 4 we found an underestimation of numerosity in the fovea and an overestimation of numerosity in the periphery. The differing directions of effects in these studies suggest that the misestimations of numerosity might depend on properties of the stimuli and experimental procedure. Nevertheless, we could show that a highly reliable and accurate integrated percept emerged despite significant differences in foveal and peripheral perception of numerosity.

The most apparent difference between the study by Valsecchi et al. (2013) and our study is certainly the constraints on eye movements: Participants were continuously fixating in the study by Valsecchi et al., whereas our participants had to execute saccades to the stimuli. As suggested by Valsecchi et al. and by Anobile et al. (2015), visual crowding might be the source of underestimating numerosity in the periphery. In turn, work by Harrison, Mattingley, and Remington (2013) has shown that the preparation of a saccade can reduce or even abolish visual crowding for the targeted stimulus. Since all our trials involved an eye movement, it is likely that visual crowding was reduced for stimuli in the periphery, which might reduce or attenuate the underestimation of numerosity in the periphery. Another factor leading to rather accurate peripheral perception might be transsaccadic recalibration (Herwig & Schneider, 2014; Valsecchi & Gegenfurtner, 2016). For example Herwig and Schneider (2014) have demonstrated that peripheral perception is biased toward a postsaccadic, foveal percept after sufficient exposure to this sequence. The interleaved integration trials within our paradigm might be sufficient to induce such transsaccadic associations. Thus, the peripheral percept might be biased toward the foveal percept expected after a saccade. Finally, the small but significant underestimation we found in the fovea might be due to the size or potentially asymmetrical shape of the attention window (Cutzu & Tsotsos, 2003; Stewart & Ma-Wyatt, 2017). Since presaccadic target stimuli in the foveal trials were small fixation crosses, the attention window might have been rather small in order to match the size of the target stimulus present at the time (Ghahghaei & Verghese, 2017). According to Cutzu and Tsotsos (2003), there is an annulus of inhibition directly surrounding the attended location. The foveal target duration might have not been sufficient for the attention window to adapt to this substantially larger numerosity stimulus present after the saccade. This small, inhibited area might have cut off a small part of the relatively large numerosity stimulus such that numerosity was perceived to be lower in foveal trials.

Importantly, the integrated percept seems to have balanced out the biases of the foveal and peripheral percepts, which led to an accurate estimate. This is in line with the assumption of the maximum-likelihood estimation model that an integrated percept should lie in between the percepts of the components. Moreover, the integrated percept should be more inclined toward the more reliable percept, which would intuitively be the foveal percept in this case. Our data do not meet this prediction, since there is a slightly higher weighting on the peripheral input for PSE values than is predicted by means of the JND values. Other factors, such as reduced crowding in the periphery or small attention windows in foveal trials, might have influenced the reliability of each percept. Furthermore, small differences in the presentation duration of the foveal stimulus might have led to an overestimation of the predicted foveal weight.

Generally, one could discuss whether participants based their perceptual judgments on numerosity or on texture density (for a review, see Anobile et al., 2016). Since we did not randomize potential cues like dot size or the size of the circular area, we cannot rule out the possibility that participants relied on texture density (Gebuis & Reynvoet, 2011, 2012). Given recent findings (Anobile et al., 2013; Cicchini et al., 2016; Zimmermann & Fink, 2016), it seems that numerosity is used for small numbers and sparse stimuli, while density is used for large numbers and dense stimuli. Estimates for the transition between numerosity and density mechanisms range between 0.25 dots/$^{\circ 2}$ (Anobile et al., 2013) and 2 dots/$^{\circ 2}$ (Cicchini et al., 2016). The densities for the stimuli we used ranged between 0.98 and 3.91 dots/$^{\circ 2}$. Given these magnitudes, it is assumable that judgments could rely on both numerosity and texture density. However, independent of which cues participants might have used here, these cues were integrated across saccades. If, as suggested by Anobile et al. (2015), foveal information is judged by numerosity but peripheral information by texture density due to crowding, it is even more interesting that such distinct modality judgments (Anobile et al., 2013) can be integrated almost optimally and lead to a more reliable judgment on numerosity than one of them alone. The same applies for Experiments 2, 3, and 4, where the brightness of the stimulus could also have been used as a cue.

Disrupting object continuity

Theoretically, transsaccadic integration could occur on a low-level, image-based representation (transsaccadic fusion) or on a high-level, abstract representation

(transsaccadic memory). According to fusion theory, pre- and postsaccadic stimuli would be fused mandatorily into one percept. This overlay implies that a change of color from black to white and vice versa should result in at least partly gray-colored dots. Since the background was also gray for the numerosity stimuli, fewer dots should have been perceived in the fused percept. In general, our results showed very little influence of stimulus changes on the accuracy of numerosity judgments, suggesting that numerosity information has been extracted from the pre- and postsaccadic stimuli separately before integration takes place.

The fact that performance was not impaired by the color change or even position change of the dots might speak for a summary-statistics mechanism being involved (Saiki & Holcombe, 2012). Summary statistics are referred to as mechanisms serving for perception given a rich input but a limited computational capacity (Attarha, 2015). These mechanisms are thought of as extracting the underlying statistics of the environmental input by finding statistical regularities among items of similar kind. For example, the task of all four experiments of this study involves summary statistics through extracting the mean of the numerosities presented. The information of the mean over all given stimuli should reach awareness to be of use; however, summary statistics are also assumed to occur in early visual processing. In the special case of visual presentation in the periphery, the brain is assumed to pool information in an area which increases its size with eccentricity (Balas, Nakano, & Rosenholtz, 2009). This pooling discards information about individual objects in a scene but extracts useful information on the ensemble. Since we found no difference in performance in most of the conditions, such a higher level mechanism is likely to apply for numerosity estimation. If there were a low-level mechanism at work—for example, every dot is assigned to a single neuron—integration performance should have gotten worse with color or position change.

Our results furthermore show that near-optimal integration across saccades is possible despite disruptions in object continuity. This is interesting because several studies have reported that the perception of differences between pre- and postsaccadic information is facilitated by blanking the target (Deubel, Schneider, & Bridgeman, 1996; Weiß, Schneider, & Herwig, 2015) or by changing target features (Poth, 2015; Poth & Schneider, 2016). Recently, transsaccadic perception of position has been modeled in a causal inference framework (Atsma, Maij, Koppen, Irwin, & Medendorp, 2016), in which pre- and postsaccadic position signals are integrated or segregated depending on the probability that they come from the same or a different source. In contrast, our findings indicate that integration can be achieved despite clear changes in other, unrelated object features. Therefore, the decision between integration and segregation seems to be more flexible and might be modulated by demands and goals of the current task set.

Neural basis

Finally, our results might help to uncover the neural basis of transsaccadic integration. One potential mechanism supporting transsaccadic integration is predictive remapping (for reviews, see Melcher & Colby, 2008; Higgins & Rayner, 2015), a phenomenon where neurons show presaccadic activity in response to visual stimuli that will be in their receptive field only after the saccade (Duhamel, Colby, & Goldberg, 1992). Predictive remapping is considered an important feature of the brain to gain perceptual stability across eye movements (for a review, see Hall & Colby, 2011). Neurons with predictive remapping were first identified in the lateral intraparietal area (Duhamel et al., 1992) and are also present in several visual areas (Nakamura & Colby, 2002; Merriam, Genovese, & Colby, 2007). However, they seem to be more prevalent in higher areas of visual processing such as V3 and V4 than in lower processing areas such as V1 and V2. Further evidence for a crucial contribution of parietal cortex comes from a study documenting impairments in transsaccadic memory due to transcranial magnetic stimulation over parietal cortex (Prime, Vesia, & Crawford, 2008). Interestingly, the parietal cortex (Harvey, Klein, Petridou, & Dumoulin, 2013)—especially the lateral intraparietal area (Roitman, Brannon, & Platt, 2007)—is also involved in the processing of number (for reviews, see Nieder & Dehaene, 2009; Piazza & Izard, 2009). Our finding that the transsaccadic integration of numerosity was not affected by changes in low-level features matches nicely with the encoding of numerosity in parietal cortex that shows a higher prevalence of remapping responses than early visual areas. Robust estimation of numerosity despite differences in stimulus properties is also a hallmark of the number sense (Nieder & Miller, 2004), indicating that numerosity can be perceived irrespective of the transient disruptions in visual processing caused by saccadic eye movements.

Conclusion

This study shows that transsaccadic information integration is possible for complex features such as numerosity. The benefit of transsaccadic integration in precision appears to remain even when object conti-

nuity is disrupted. This identifies transsaccadic integration as a highly robust mechanism that helps the visual system to create a stable perception of our environment. Numerosity perception per se becomes more accurate with the integration of peripheral and foveal numerosity information compared to one of the inputs alone. This stresses the assumption that transsaccadic integration not only maximizes information gain but also alleviates miscalibrations of peripheral and foveal vision to maintain a stable perception of our environment.

Keywords: saccades, *numerosity*, *perceptual stability*, *transsaccadic integration*, *transsaccadic fusion*, *transsaccadic memory*

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Footnote

[1] With this paradigm, we cannot make assertions about the actually perceived numerosity, only about the momentary relation of the stimuli and the percept. For instance, if a participant consistently overestimated every stimulus seen (e.g., perceived numerosities of 22, 32, 42, 46, 52, 58, 62, 72, and 82 instead of 20, 30, 40, 44, 50, 56, 60, 70, and 80), he or she would still show a PSE close to 50 (the mean numerosity would still be rated as the PSE).

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Study II

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Stronger saccadic suppression of displacement and blanking effect in children

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Humans do not notice small displacements to objects that occur during saccades, termed saccadic suppression of displacement (SSD), and this effect is reduced when a blank is introduced between the pre- and postsaccadic stimulus (Bridgeman, Hendry, & Stark, 1975; Deubel, Schneider, & Bridgeman, 1996). While these effects have been studied extensively in adults, it is unclear how these phenomena are characterized in children.
A potentially related mechanism, saccadic suppression of contrast sensitivity—a prerequisite to achieve a stable percept—is stronger for children (Bruno, Brambati, Perani, & Morrone, 2006). However, the evidence for how transsaccadic stimulus displacements may be suppressed or integrated is mixed. While they can integrate basic visual feature information from an early age, they cannot integrate multisensory information (Gori, Viva, Sandini, & Burr, 2008; Nardini, Jones, Bedford, & Braddick, 2008), suggesting a failure in the ability to integrate more complex sensory information. We tested children 7 to 12 years old and adults 19 to 23 years old on their ability to perceive intrasaccadic stimulus displacements, with and without a postsaccadic blank. Results showed that children had stronger SSD than adults and a larger blanking effect. Children also had larger undershoots and more variability in their initial saccade endpoints, indicating greater intrinsic uncertainty, and they were faster in executing corrective saccades to account for these errors. Together, these results suggest that children may have a greater internal expectation or prediction of saccade error than adults; thus, the stronger SSD in children may be due to higher intrinsic uncertainty in target localization or saccade execution.

Introduction

Humans can execute multiple saccadic eye movements per second. With every saccade, the presaccadic stimulus features and location must be reconciled with their postsaccadic counterpart in order to maintain a stable percept of the world. The visual system may achieve this transsaccadic perceptual stability by integrating pre- and postsaccadic feature information (Demeyer, Graef, Wagemans, & Verfaillie, 2010a; Ganmor, Landy, & Simoncelli, 2015; Wijdenes, Marshall, & Bays, 2015; Wolf & Schütz, 2015; Stewart, Valsecchi & Schütz, in press) or location information (Cicchini, Binda, Burr, & Morrone, 2013; Prime, Niemeier, & Crawford, 2005), or by suppressing small displacements that occur during the saccade (Bridgeman, Hendry, & Stark, 1975). However, it is unknown when such mechanisms develop. While many visual processes such as integration and segmentation of basic visual features develop in the first few years of life (for review, see Braddick & Atkinson, 2011), other integrative processes such as optimal multisensory integration are still developing up until 8 to 10 years of age (Gori, Viva, Sandini, & Burr, 2008; Jovanovic & Drewing, 2014; Nardini, Jones, Bedford, & Braddick, 2008), and performance on more cognitively demanding saccade tasks such as antisaccades continues to develop until the age of 15 (Munoz, Broughton, Goldring, & Armstrong, 1998). In this study, we focus on the development of one process that contributes to transsaccadic perceptual stability—saccadic suppression of displacement (SSD)—and compare SSD and the blanking effect between children 7 to 12 years old and adults 19 to 25 years old. Measuring SSD in children gives us an

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insight into when transsaccadic integrative processes may develop; measuring the blanking effect allows us to test whether the same information may also be segregated when correspondence between pre- and postsaccadic stimuli is broken. We additionally relate perceptual measures to saccade error metrics to explain how greater saccade variability may result in greater SSD.

Saccadic suppression of displacement and the blanking effect

SSD refers to the inability of observers to detect small stimulus displacements that occur during a saccade (Bridgeman et al., 1975). SSD is strongest when the stimulus displacements occur in an elliptical area along the axis of saccade direction (Wexler & Collins, 2014), and scales with saccade amplitude, such that larger displacements are undetected for larger saccade amplitudes (Bridgeman et al., 1975; Li & Matin, 1990; Li & Matin, 1997).

SSD is thought to arise from several aspects of visuomotor and perceptual processing. Contrast sensitivity during a saccade is strongly reduced, due to several factors, such as retinal image blur caused by high eye velocity (Burr & Ross, 1982; Castet, Jeanjean, & Masson, 2002; Castet & Masson, 2000; Ilg & Hoffmann, 1993); masking by the clear and strong input before and after the saccade (Campbell & Wurtz, 1978; Duyck, Collins, & Wexler, 2016), and an active reduction of sensitivity (Braun, Schütz, & Gegenfurtner, 2017; Burr, Holt, Johnstone, & Ross, 1982; Burr, Morrone, & Ross, 1994; Diamond, Ross, & Morrone, 2000). This phenomenon is called saccadic suppression of contrast sensitivity (SSCS). When a stimulus changes its position during fixation, a highly informative motion transient can be obtained (Tynan & Sekuler, 1982); however, if the displacement happens during a saccade, this transient is suppressed due to SSCS. The visual system must presumably then compare the observed presaccadic target position to the observed postsaccadic target position (evaluation on the underlying process can be found in the paragraphs below). The localisation ability of the visual system, however, is imperfect and diminishes with increasing eccentricity (Anderson & Yamagishi, 2000; Hess & Hayes, 1994; Levi & Tripathy, 1996; Michel & Geisler, 2011; Westheimer, 1982; White, Levi, & Aitsebaomo, 1992). The visual system could also use position information that comes from the execution of the eye movement itself, but this is itself noisy (Abrams, Meyer, & Kornblum, 1989; Frost & Pöppel, 1976; van Beers, 2007; van Opstal & Gisbergen, 1989; Vitu, Casteau, Adeli, Zelinsky, & Castet, 2017). Given these limitations, it does not seem surprising that the visual system has difficulties correctly perceiving intra-saccadic displacements. In addition, sudden position changes of objects are statistically unlikely, and the visual system is believed to have a prior expectation that results in a bias for perceiving the environment as stable (MacKay, 1972).

The questions of why there is SSD and why we perceive no major motion disruptions due to our rapid eye movements are two sides of the same coin. This question can also be framed as: "How and under which conditions does the visual system draw connections between the disconnected pre- and postsaccadic inputs?" For the "how" part of the question, research suggests that, instead of presaccadic information being overwritten or disregarded by the arrival of more reliable postsaccadic information, pre- and postsaccadic feature information can be integrated to form a single percept of increased precision, which is referred to as transsaccadic integration. It has been found that visual features such as orientation (Ganmor et al., 2015; Stewart & Schütz, 2018a; Stewart & Schütz, 2019a; Stewart & Schütz, 2019b; Wolf & Schütz, 2015), color (Schut, Van der Stoep, Fabius, & Van der Stigchel, 2018; Stewart & Schütz, 2018b; Wijdenes et al., 2015), and numerosity (Hübner & Schütz, 2017) are integrated and weighted by the reliability of each single input, resulting in the perception of the weighted sum that is more precise than the perception of each single input (Ernst & Bülthoff, 2004). Pre- and postsaccadic location information can also be integrated, which can aid target localization (Atsma, Maij, Koppen, Irwin, & Medendorp, 2016; Cicchini et al., 2013; Niemeier, Crawford, & Tweed, 2003; Prime et al., 2005; Vaziri, Diedrichsen, & Shadmehr, 2006; Zimmerman & Lappe, 2010). SSD can be considered to be the result of the integration of pre- and postsaccadic location information and as a result, a loss of access to the individual estimations (e.g., Niemeier et al., 2003).

However, transsaccadic feature integration is not necessarily an automatic process and may not occur without specific task demands (Stewart & Schütz, 2018b; Stewart & Schütz, 2019b; Stewart, Valsecchi & Schütz, in press); similarly, it is not mandatory for pre- and postsaccadic location information to be fully integrated. This leads to the "under which conditions" part of the above question. SSD can be explained in terms of two models that describe the conditions under which integration of pre- and postsaccadic location information occurs (Atsma et al., 2016; Niemeier et al., 2003). The first model posits that integration decreases as the discrepancy between pre- and postsaccadic location information increases, making perception of displacements more accurate (Niemeier et al., 2003). Specifically, Niemeier and colleagues suggested that the threshold after which integration declines may be determined by both a prior assumption of the visual system's intrinsic noisiness, and a prior assumption of extrinsic stability. Their model states that small discrepancies in pre- and postsaccadic location

information are attributed to internal noise, such as (unplanned) variability in saccade landing positions. The model predicts that the more uncertain a system is about its own sensorimotor state, the less likely it is to attribute displacements to an external cause.

The second model incorporates the two extreme assumptions about the world: Either the world is stable, which will lead to full integration, or it is not, which causes the inputs to be kept separate (Atsma et al., 2016). Evidence supporting either of these two options is weighted through a causal inference mechanism (Atsma et al., 2016; Körding, Beierholm, Ma, Quartz, Tenenbaum, & Shams, 2007; Wozny, Beierholm, & Shams, 2010). This model can also predict participant behavior and suggests similar conditions for SSD as the first model. However, Atsma et al. (2016) additionally showed that the strength of SSD increases with decreasing quality of location information obtained from an object, and their model can account for those effects by incorporating localization uncertainty as a factor influencing the stability assumption. Whereas Atsma et al. (2016) demonstrated that their model can explain more variability due to location information quality, the models by both Niemeier et al. (2003) and Atsma et al. (2016) suggest that increased SSD is due to increased sensory or sensorimotor uncertainty. Considering children as potential candidates for having increased sensory or sensorimotor uncertainty (see section on Development of saccadic suppression and information integration), both models make equivalent predictions that suggest stronger SSD in children.

SSD is a robust phenomenon, but it can also be disrupted. Deubel and colleagues found that blanking the saccade target for 50 to 300 ms immediately after the initial saccade seemed to reduce SSD (Deubel, Schneider, & Bridgeman, 1996). The authors named this decrease in displacement detection threshold the blanking effect. It might seem counterintuitive that making the target temporarily unavailable to the observer increases the likelihood of perceiving a displacement of the target; however, this effect can again be explained by a change in the assumption of external stability. The visual system might consider the disappearance of the saccade target upon landing as key evidence for a change in the world. That might strongly reduce, or even nullify a stability assumption, such that discrepancies in location information (e.g., due to a displacement of the saccade target) are assigned to external causes rather than internal noise; hence, thresholds for perceiving displacements are reduced (Deubel et al., 1996; Deubel, Bridgeman, & Schneider, 1998; Niemeier et al., 2003). Niemeier et al. (2003) were able to simulate the blanking effect by adjusting the stability assumption as a free parameter in their model. SSD is also reduced by other manipulations violating the stability assumption, such as task-irrelevant orthogonal displacements (Wexler & Collins, 2014), contrast polarity, or object identity changes (Demeyer, Graef, Wagemans, & Verfaillie, 2010b; Tas, Moore, & Hollingworth, 2012).

A second view assigns the blanking effect to a change in the quality or processability of location information (Born, 2019; Ziesche, Bergelt, Deubel, & Hamker, 2017; Zimmermann, Morrone, & Burr, 2013). Specifically, the onset of the postsaccadic location information might convey critical evidence for a displacement (Born, 2019). Because postsaccadic blanking delays the onset of the postsaccadic location information to a time after saccadic suppression of contrast sensitivity, this information can be properly obtained in the blanking condition. This could mean then that either the quality of the location information is increased, leading to reduced SSD (Matsumiya, Sato, & Shioiri, 2016; but see Takano, Matsumiya, Tseng, Kuriki, Deubel, & Shioiri, 2020), or that enough time is provided for the visual system to fully process the location information (Ziesche et al., 2017). This second interpretation can explain SSD and blanking effects without the need for a stability assumption. However, it fails to explain several features of SSD: the elliptical window of SSD along the saccade trajectory (Wexler & Collins, 2014), the alleviation of SSD due to task-irrelevant feature changes (Demeyer et al., 2010b; Tas et al., 2012; Wexler & Collins, 2014), and illusory displacements that occur for a blanked target that appears adjacent to a target that was not blanked (Deubel, 2004; Deubel et al., 1998; Deubel, Koch, & Bridgeman, 2009; Higgins & Wang, 2009).

Given that current evidence from the literature is in favor of the explanation based on a violation of the stability assumption, a condition including a postsaccadic blank can serve as a measure of SSD when the stability assumption is rejected (Niemeier et al., 2003). This would substantially reduce the influence of sensory or sensorimotor uncertainty on SSD that might otherwise be higher in children compared to adults. What exactly can be expected from measuring SSD with and without a postsaccadic blank in children is evaluated in the following section.

Development of saccadic suppression and information integration

SSD and the blanking effect are robust phenomena that have been studied extensively in adults; however, we do not know whether children also experience these effects or when the potential mechanisms underlying these effects develop. Basic visual perception develops within the first few years of age (Braddick & Atkinson, 2011), but it is unclear when transsaccadic perceptual

processes develop in children; their development may rely more on the development of the oculomotor system than on the development of visual perception and may also reflect the greater variability in saccade execution that accompanies this development. The saccade planning system seems to still be developing up until around 8 years of age. Saccade latencies decrease with age (Bucci & Seassau, 2012; Cohen & Ross, 1977; Munoz et al., 1998; Salman et al., 2006) and reach the same level as adults by the age of 12 (Fukushima, Hatta, & Fukushima, 2000). Saccade gain seems to increase with age (Bucci & Seassau, 2012), with some studies indicating that children reach adult-like performance by the age of 8 (Munoz et al., 1998; Salman et al., 2006). This developing oculomotor control may result in greater uncertainty in saccade planning or execution. The models of Atsma et al. (2016) and Niemeier et al. (2003) would predict that this increased uncertainty may lead to greater SSD. Indeed, this seems to be the case for one such transsaccadic perceptual phenomenon, as saccadic suppression of contrast sensitivity is even more pronounced in children than in adults, with children showing three times more suppression than adults (Bruno, Brambati, Perani, & Morrone, 2006). This could be due to a stronger need to suppress information due to uncertainty in developing oculomotor functions (Bruno et al., 2006; Niemeier et al., 2003). If the development of SSD is similar to saccadic suppression of contrast sensitivity, then we would expect to see stronger SSD in children than adults. Studies on the development of multisensory integration may also give us insight as to when transsaccadic integrative processes may develop, because the integration of transsaccadic information and multisensory integration have been shown to rely on the same principles of optimal cue combination (Ganmor et al., 2015; Wolf & Schutz, 2015). Transsaccadic integration has not been studied in children; however, studies into the development of multisensory information suggest a rather late development. Nardini et al. (2008) showed that, while adults could optimally integrate and weight landmark and non-visual self-motion cues in a navigation task, children between 4 and 8 years of age failed to integrate the cues. Similarly, the integration of visuohaptic information develops only after the age of 8 to 10, before which children rely on a single modality (Gori et al., 2008). This late development may be due to the ongoing process of calibration to account for perceptual and sensorimotor development, or a failure to develop correspondence between different signals (Ernst, 2008; Gori et al., 2008). This latter idea was supported by Jovanovic & Drewing (2014), who found that children 6 years of age can integrate visuohaptic information, but only when the discrepancy between the stimuli was small, and when the stimuli were more likely to be attributed to a single origin. Calibration of perceptual and sensorimotor processes and causal correspondence are both elements that may play a role in integrating pre- and postsaccadic position information (Atsma et al., 2016; Niemeier et al., 2003). The processes underlying transsaccadic information integration may also still be subject to a sensorimotor and perceptual calibration process in children. Integration of information during SSD may reflect integration processes involved in multisensory integration, in which case we would expect to see less integration of information and therefore less SSD in children than adults.

Rationale of this study

This study aimed to investigate the development of mechanisms supporting perceptual stability by comparing SSD and the blanking effect in children 7 to 12 years old and adults 19 to 25 years old. We aimed to make inferences about how SSD works by measuring a population in whom SSD has not yet fully developed. We measured SSD by displacing the saccade target during the saccade, with and without an intervening blank between the pre- and postsaccadic stimulus. The introduction of a postsaccadic blank allowed us to measure a reduction in SSD (Bridgemann et al., 1975); with the addition of the blank, we would expect that integration may also be reduced or may not occur. To further investigate the mechanisms underlying SSD, we related these perceptual measures to measures of oculomotor performance. Saccade landing accuracy and precision allowed us to determine the amount of uncertainty in saccade planning and execution, and corrective saccade latencies were used as a measure of internally predicted saccade error.

Methods

Participants

Seventeen adults and seventeen children who were unaware of the purpose of the study participated in the experiment. We excluded two adults: one who did not respond in accordance with the task, so psychometric functions were not well defined, and one who showed a strong bias to respond by saccade direction. Two children were excluded from analysis, both of whom responded by saccade direction, despite repeated attempts at instruction. Fifteen adults (11 females, four males; mean age 23 years, range 19–25 years) and 15 children (nine females, six males; mean age 9 years, range 7–12 years) were included for analysis (Figure 1B). The ages of the children were chosen based on multisensory integration literature, which suggests

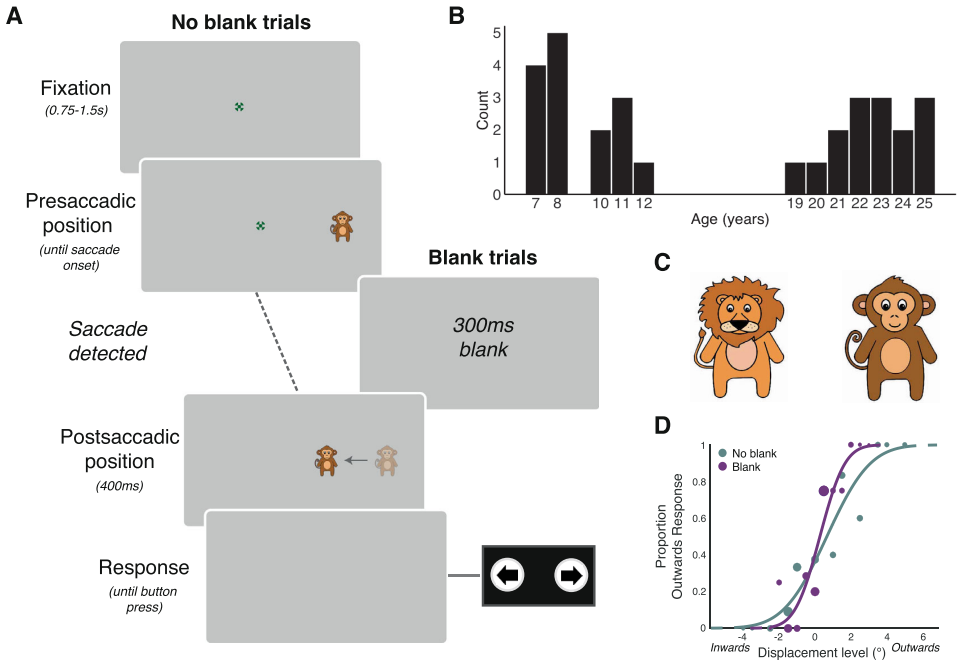

Figure 1. Experiment procedure and stimuli. (A) Trial sequence. Participants fixated a central fixation stimulus. Upon key press and after a random interval between 0.75 and 1.5 seconds, the target stimulus appeared at the presaccadic location. When the saccade was detected, the stimulus jumped either inward or outward either immediately (no-blank trials) or after 300 ms of blank screen (blank trials). Participants used a response box to indicate the direction of the jump. (B) Histogram of participant ages. (C) Monkey and lion stimuli. (D) Example psychometric functions for one participant (8 years old) showing fitted cumulative Gaussian distributions for blank (purple) and no-blank (turquoise) conditions.

that this range is interesting for the development of sensory calibration (Gori, 2015).

Adult participants were Marburg University students and were reimbursed for participation. Children were recruited via flyers inside and outside Marburg University and were accompanied by at least one legal guardian on the day of participation. Children were reimbursed with money and a toy of choice. The experiment was conducted in accordance with the tenets of the Declaration of Helsinki (1964) and approved by the local ethics committee of the Psychology Department at Marburg University (proposal number 2015-35k). All participants and their legal guardians in the case of the children gave informed consent. All participants had normal or corrected-to-normal vision.

Equipment

Stimuli were presented using a back-projection setup, using a PROPixx projector (VPixx Technologies, Saint Bruno, QC, Canada), with a resolution of 1920 × 1080 and a refresh rate of 120 Hz, projected onto a 91 × 51-cm screen from Stewart Filmscreen (Torrance, CA). Viewing distance was 106 cm. The screen was calibrated to ensure a linear gamma correction and to correct the central hot spot, and it had a background luminance of 92 cd/m^2. The CIE 1931 x, y coordinates of the screen were (0.6722, 0.3222), (0.1707, 0.7390), and (0.1515, 0.0464) for red, green, and blue, respectively. Eye movements were recorded using an EyeLink 1000+ (SR Research Ltd., Kanata, ON, Canada), with a sampling rate of 1000 Hz. The experiment was presented with custom written software in MATLAB (National Institutes of Health, Bethesda, MD), using Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and the EyeLink Toolbox (Cornelissen et al., 2002). Participants responded using a Black Box Toolkit USB response pad (Black Box ToolKit Ltd., Sheffield, UK). All participants used a chin and forehead rest for head stabilization.

Eye tracker calibration

The eye tracker was calibrated using the participant's right eye for nine locations (marked by a fixation stimulus) in a grid array with one location at the center

of the screen and the remaining with an eccentricity of 17° of visual angle on the horizontal and/or 10° on the vertical axis. The experimenter confirmed gaze position at each location manually while ensuring that each difference between computed gaze position and stimulus location was below 0.75° of visual angle during validation. The calibration procedure was conducted before the start of the experiment and whenever the experimenter noticed that a participant needed a break (by verbal or nonverbal signals), which could be every 20 trials for the youngest participants. Despite children having to be reminded more frequently to restrain head and body movements, after successful instruction gaze position errors were about equal for children and adults across calibration procedures. In addition to the calibration procedure, at the start of each trial a drift check was implemented that was manually confirmed by the participant using the two lowest-positioned of four buttons on the response box.

Stimuli

The initial fixation stimulus was a combination of bull's-eye and crosshair, which has been demonstrated to be especially effective for maintaining stable fixation on a screen (Thaler, Schutz, Goodale, & Gegenfurtner, 2013). The fixation stimulus was 0.15° × 0.6° of visual angle. The color of the fixation stimulus was chosen randomly out of an array of colors generated in Derrington–Krauskopf–Lennie (DKL) color space (Derrington, Krauskopf, & Lennie, 1984), with randomized polarity and isoluminance toward the gray background to avoid the build-up of afterimages. Target stimuli were two animal cartoons designed to be appealing to the children in order to motivate them (Figure 1C). The monkey was 2.39° high and 1.76° wide. The lion was 2.51° high and 1.72° wide. Colors were chosen to match the animal and differed in luminance (Figure A4).

Procedure and design

The aim of our experiment was to measure SSD with and without a postsaccadic blank in children and adults. In order to get children interested in the experiment and sufficiently motivated to sit still through all trials, we first familiarized them with a jungle theme, and the subsequent task instructions were embedded in an imaginative role play where the child took on the role of a researcher investigating the jumping behavior of animals appearing in the jungle.

To start a trial, participants fixated a central fixation stimulus and simultaneously pressed a button on the response box. After a random interval varying between 0.75 and 1.5 seconds (during which time fixation was maintained), one of the animals appeared at an 8° or 10° eccentricity, to either the left or right of central fixation (presaccadic target position) (Figure 1A). Applying an overlap paradigm (Saslow, 1967), the fixation stimulus remained on-screen with the presaccadic target and was removed either after an additional 200 ms following the fixation interval or when the presaccadic target was removed. The presaccadic target was removed as soon as the eye position exceeded 2° with respect to the screen center and reappeared either immediately (no-blank trial) or 300 ms later (blank trial) at the postsaccadic target location. The postsaccadic target location was shifted on the horizontal axis relative to the presaccadic target position by a magnitude and direction determined by an adaptive staircase procedure. This procedure was composed of three independent, randomly interleaved staircases for each condition, with a constant step size of 2.5° for the no-blank condition and 1.5° for the blank condition (per Ostendorf, Liebermann, & Ploner, 2010). The staircases started at an initial displacement level of 0°, –4° (left), and 4° (right) in the no-blank condition, or 0°, –2° (left), and 2° (right) in the blank condition. The step size was either added (rightward) or subtracted (leftward) from the current displacement level whenever a participant responded left or right perceived displacement, respectively. This procedure enabled us to measure the point of subjective stationarity and the just noticeable difference (JND) while keeping the total number of trials low.

The postsaccadic target was presented for a duration of 400 ms. The subsequent empty screen prompted the participant to respond whether they perceived a displacement direction to the left or to the right. Participants were told to guess when they did not perceive any displacement.

For motivation purposes, after every 10 trials, an illustration of a clipboard appeared indicating the number of animals observed thus far. Whenever a participant blinked within a trial, a sound of the animal running away was played together with a voice recording to remind the participant not to blink. When children were being tested, the experimenter remained inside the experimental room throughout the experiment and prompted a break every 30 trials, or whenever it seemed appropriate. Each participant completed at least 144 trials.

Analyses

Saccade onsets and offsets were detected offline using the EyeLink 1000+ algorithm (velocity threshold = 22°/s, acceleration threshold = 3800°/s^2). Saccade latencies of the main/initial saccades were defined as the first sample after target onset in which a saccade was detected; likewise, saccade offsets were defined as the last sample after saccade onset in which a saccade was

detected plus 10 ms (to bypass longer post-oscillation times). Corrective saccades were defined as saccades with onset at least 50 ms after initial saccade offset (no-blank trials) or 50 ms after postsaccadic stimulus appearance (blank trials). In addition, for a saccade to be considered a corrective saccade, the landing position had to be closer to the postsaccadic target position than the landing position of the initial saccade.

Trial exclusions

We excluded trials with erroneous saccades. These were defined as trials without any saccades, with saccades that were halted such that the displacement happened when the eye was stationary, with initial saccades directed opposite to target position, or with blinks occurring within 300 ms of target onset. We included all trials with saccade latencies between 50 and 1000 ms to account for the large variability in saccade latency within children (Munoz et al., 1998). The overall percentage of trial exclusions was 8% ± 7% for adults and 18% ± 11% for children (mean ± standard deviation), resulting in 142 ± 21 trials across all participants. Trial exclusions for each criterion and participant can be found in the Appendix (Tables A1 and A2).

Psychometric functions

To obtain psychometric functions (see example in Figure 1D), perceptual choices were converted into proportion outward responses for each displacement level tested (displacement levels were converted into inward/outward displacements with respect to screen center). A cumulative Gaussian was fitted to the data using the psignifit 4.0 toolbox for MATLAB (Schütt, Harmeling, Macke, & Wichmann, 2016). The point of subjective stationarity was estimated as the level of displacement corresponding to 50% outward responses. JNDs were defined as the standard deviation of the cumulative Gaussian, with lower JNDs indicating higher precision of displacement perception.

To assess the goodness of fit for each psychometric function we calculated the deviance (D) normalized by the number of displacement levels tested (listed in Tables A1 and A2). Deviance is a log-likelihood ratio between a saturated model and the fitted psychometric function and is recommended as a goodness-of-fit measure for binomial data (Schütt et al., 2016; Wichmann & Hill, 2001). To verify that fits were equally good for both blanking conditions, we performed a mixed analysis of variance (the assumption of normality was checked using a Lilliefors test, and the assumption of homogeneity of variance was checked using a Levene test) for the normalized deviances and found no significant effect for the within-factor blanking condition, $F(1, 28) = 0.37$, $p = 0.5486$; a significant effect for the between-factor age group, $F(1, 28) = 12.24$, $p = 0.0016$; and no significant interaction between blanking condition and age group, $F(1, 28) = 2.39$, $p = 0.1333$. This confirms our expectation that psychometric function fits are less reliable for children, D_norm = 0.73 ± 0.30, than for adults, D_norm = 0.43 (0.34), due to a lower number of valid trials (also listed in Tables A1 and A2). However, as can be seen in Figures A1 and A2, even the psychometric functions for children achieved a reasonable fit. Most importantly, the reliability of fits did not differ between blank and no-blank conditions for either of the participant groups.

Statistical analyses

Linear models were calculated using R (R Foundation for Statistical Computing, Vienna, Austria) (based on Chambers, 1992; Wilkinson & Rogers, 1973). Linear mixed models were calculated in R using the nlme package (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2020). Pairwise comparisons were calculated in R using the emmeans package (Lenth, Buerkner, Herve, Love, Riebl, & Singmann, 2020). Bayes factors were calculated using the BayesFactor package in R (Morey, Rouder, Jamil, Urbanek, Forner, & Ly, 2019). For linear models, Bayes factors were calculated using the default inverse gamma prior. For linear mixed modes, Bayes factors were calculated using default priors (inverse gamma prior on the regression and Jeffreys prior on effects). Bayes factors for main effects were calculated as the ratio of evidence for the model containing only that factor versus the null (intercept and random effects only) model. Interactions were calculated as the full model with interaction term versus the model containing main effects with no interaction term. For t-tests, Bayes factors were calculated using default Jeffreys prior on variance and Cauchy prior on standardized effect size (Rouder, Speckman, Sun, Morey, & Iverson, 2009).

For linear models and linear mixed models, fixed effects of age group (children or adults) and blanking condition (blank or no-blank) were categorically coded, with children coded as baseline contrast factor level for age group comparisons and no blank coded as baseline contrast factor level for blanking condition comparisons. For mixed-model analyses, random effects structures are described in the results section. Assumptions of model fits (normality of residuals and homoscedascity) were checked using standard graphical procedures (Gelman & Hill, 2006; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We report statistics on the fixed effects of each model: F statistic, p value, and Bayes factors (BF_{10} indicates evidence against the null hypothesis). Statistical tests were performed on the data shown in the corresponding figures, such that there

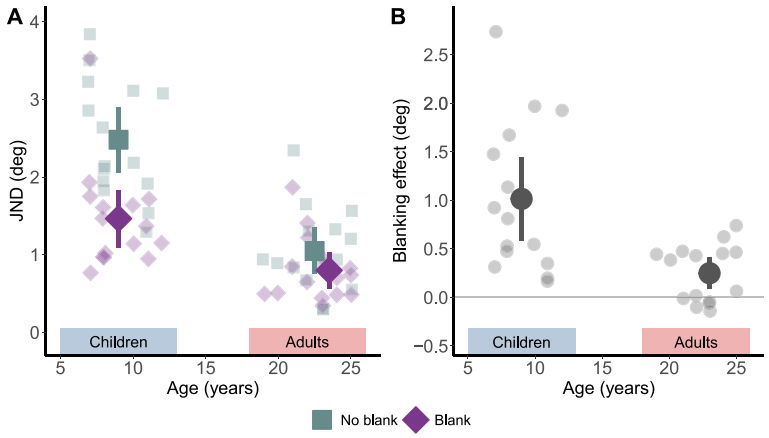

Figure 2. Perceptual performance. (A) JNDs for no-blank (turquoise squares) and blank (purple diamonds) conditions. (B) Blanking effect (difference between blank and no blank conditions). Individual subjects are shown by age in small symbols and means for children and adults in larger symbols (where mean symbols are offset on the *x*-axis to avoid overlap, they do not reflect mean age). Error bars are 95% CIs.

was one data point per subject. There was necessarily only one JND per participant; saccade latencies and landing errors were calculated as mean or median per participant.

Results

Perceptual results

Saccadic suppression of displacement for children versus adults

To determine how JNDs changed across age and blanking condition (Figure 2A), we used a linear mixed model, with fixed effects of age group (children or adults) and blanking condition (blank or no blank), and random intercepts and slopes for blanking condition (blanking condition was nested within participant). There was a significant main effect of age group, $F(1, 28) = 28.76$, $p < 0.0001$, $BF_{10} = 931.07$ (extreme evidence), demonstrating that JNDs were lower for adults than for children, suggesting that SSD is stronger for children than adults (Figure 2). There was a significant main effect of blanking condition, indicating that JNDs differed significantly between blanking conditions across both age groups, $F(1, 28) = 34.6$, $p < 0.0001$, $BF_{10} = 607.95$ (extreme evidence). There was a significant interaction between blanking condition and age group, $F(1, 28) = 12.7$, $p = 0.013$, $BF_{10} = 18.91$ (strong evidence), suggesting that the difference between blank and no-blank conditions differed between children and adults. Post hoc pairwise comparisons with a Holm correction for multiple comparisons showed a significant difference between blanking conditions for children: $t(28) = 6.68$, $p < 0.0001$.

Blanking effect for children versus adults

To further clarify how blanking affected SSD, we calculated the blanking effect as the difference in JNDs between blank and no-blank conditions (Figure 2B). This is essentially the same analysis as the interaction effect above; however it allows for a direct comparison of blanking effect with previous studies (Table A3). The mean blanking effect for adults was 0.25° ($SD = 0.30°$) and for children was 1.02° ($SD = 0.78°$). A linear model with fixed effect of age group showed a significant difference in blanking effect between children and adults, $F(1, 28) = 12.7$, $p = 0.0013$, $BF_{10} = 24.44$ (strong evidence), demonstrating that children had a larger blanking effect than adults. To ensure that this was not due to the relative difference in absolute JND levels between children and adults, we also compared the relative blanking effect for the two age groups. The relative blanking effect was calculated for each participant as the *difference* in JND between blank and no-blank conditions for that participant, divided by the *mean* of the blank and no-blank JND for the participant: $(JND_{Blank} - JND_{NoBlank})/[(JND_{Blank} + JND_{NoBlank})/2]$. The difference between children and adults was again still significant, $F(1, 28) = 4.93$, $p = 0.035$, $BF_{10} = 2.06$ (anecdotal evidence), showing that children had a larger blanking effect than adults.

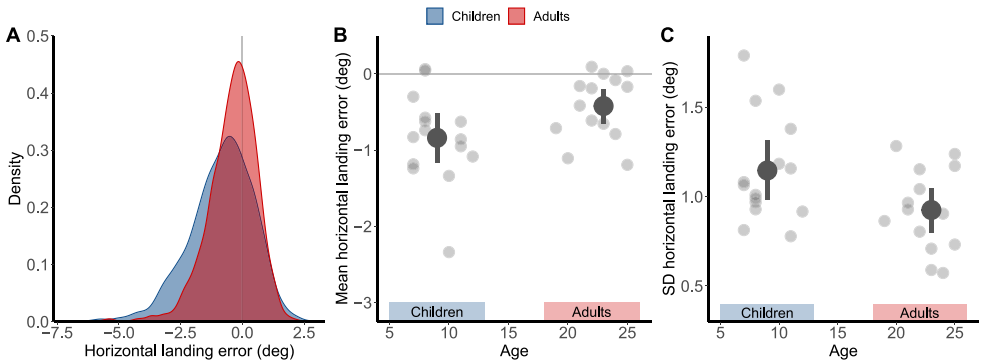

Figure 3. Horizontal landing error for children (blue) and adults (red). (A) Horizontal landing error (negative values represent undershoot of target), as density distributions. (B) Mean horizontal landing error by age. (C) SD horizontal landing error by age. In (B) and (C), small gray symbols represent individual subjects, and large symbols represent mean values for children (blue) and adults (red). Error bars are 95% CIs.

	Mean (SD), °		Median (IQR), ms	
	Horizontal landing error – initial saccade	Vertical landing error – initial saccade	Initial saccade latency	Corrective saccade
Children				
No blank	–0.87 (1.1)	–0.19 (0.49)	191.1 (134.8)	150.7 (54)
Blank	–0.80 (1.2)	–0.18 (0.48)	182.5 (142.5)	180.6 (92.8)
Adults				
No blank	–0.41 (0.93)	–0.15 (0.35)	161.5 (78)	199.5 (84.9)
Blank	–0.43 (0.92)	–0.14 (0.34)	163.2 (83)	213.2 (85.6)

Table 1. Summary saccade metrics. Mean and standard deviation landing error and median and interquartile range (IQR) initial and corrective saccade latency are reported.

Eye movement results

Accuracy and precision of initial saccades

Given that the SSD may be related to the precision and accuracy of saccades in the direction of displacement (Wexler & Collins, 2014), we examined how horizontal landing error for the initial saccade differed across age (Figures 3A and 3B; Table 1). We compared saccade accuracy (mean horizontal landing error) between age groups (children or adults) with a linear model. There was a significant effect of age group, $F(1, 28) = 5.05$, $p = 0.033$, $BF_{10} = 2.14$ (anecdotal evidence). Both groups showed an undershoot of the saccade target; a one-tailed t-test showed that mean horizontal landing position was significantly different from 0 (the directional t-test was used to compare whether the mean was less than 0). For children, $t(14) = -5.48$, $p < 0.0001$, BF_{10} (evidence mean < 0/evidence mean not < 0) = 24815.96 (extreme evidence). For adults, $t(14) = -4$, $p = 0.0007$, BF_{10} (evidence mean < 0/evidence mean not < 0) = 803.1 (extreme evidence). Children showed on average a larger undershoot than adults. Similarly, we compared saccade precision (variability in horizontal landing error), showing a significant decrease with age group, $F(1, 28) = 5.26$, $p = 0.029$, $BF_{10} = 2.31$ (anecdotal evidence). This suggests that initial saccade accuracy and precision were greater in adults than children.

Saccade accuracy and blanking effect

To test whether saccade accuracy was related to the magnitude of the blanking effect, we used a linear model to test whether horizontal landing error in the no-blank condition was predictive of the magnitude of blanking effect (blanking effect as a function of log horizontal landing error to correct the assumption of normally distributed residuals). There was a significant relationship between horizontal landing error and blanking effect, $F(1, 28) = 8.93$, $p = 0.0058$, $BF_{10} = 7.71$ (moderate evidence). This suggests that as

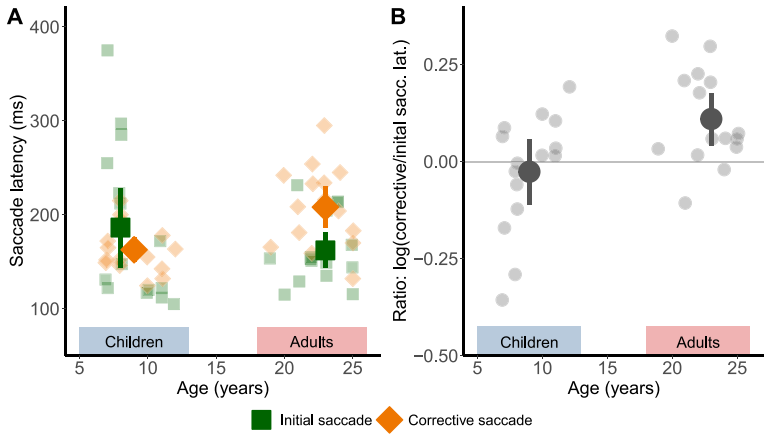

Figure 4. Initial versus corrective saccade latencies. (A) Initial (green squares) and corrective (orange diamonds) saccade latencies by age. (B) Log ratio of corrective to initial latencies by age. The ratio is calculated as the log of corrective latency divided by initial saccade latency. In (A) and (B), individual subjects are shown by age in small symbols and means for children and adults in larger symbols (mean symbols are offset on the *x*-axis to avoid overlap and do not reflect mean age). Error bars are 95% CIs.

saccade accuracy decreased the amount of postsaccadic target displacement tolerated increased.

Shared noise in perception and eye movements

We based our analysis on the assumption that expectations of internally caused errors are intrinsic to a participant, rely on long-term experience, and would not change on a trial-by-trial basis. It is, however, entirely possible that perceptual performance also correlates with motor performance on a given trial—for example, due to shared noise sources (Stone & Krauzlis, 2003; Liston & Stone, 2008; but see Gegenfurtner, Xing, Scott, & Hawken, 2003). In other words, high internal noise on a given trial might affect both perception of displacement and saccade landing error. To determine to what extent a correct or incorrect perceptual response can be predicted based on the horizontal landing error of the initial saccade, we conducted a receiver operating characteristic (ROC) curve analysis over all blank and no-blank trials that could be labeled as correct or incorrect based on response and displacement direction (zero-displacement trials were discarded). We calculated the areas under the ROC curves (AUCs) with a baseline of 0.5 (AUC values above the baseline indicate a predictability above chance). For children (no blank = 0.56, blank = 0.55) and for adults (no blank = 0.57, blank = 0.53), horizontal landing error could marginally predict response correctness with slightly higher predictability for the no-blank condition. While we think that this analysis points to a limited contribution of shared noise to perceptual and motor performance, the relatively small AUC values do not contradict the assumption of experience-based expectations as being the main cause for the blanking effect difference between children and adults.

Initial and corrective saccade latencies

Previous studies have shown that both initial and corrective saccade latencies decrease as children become older (Cohen & Ross, 1978; Munoz et al., 1998; Salman et al., 2006). To see if this was also the case in this study, we compared initial and corrective saccade latencies across age (Figure 4A; Table 1). We used a linear mixed-effects model, with fixed effects of age group (children or adults), saccade type (initial or corrective saccade), and blanking condition (blank or no-blank), and random intercepts and slopes for subjects (blanking condition nested within subject). Saccade latency was log-transformed to meet the assumption of normality of residuals for the test (Gelman & Hill, 2006). There was no significant main effect of age group, $F(1, 28) = 0.78$, $p = 0.39$, $BF_{10} = 0.44$ (anecdotal evidence for the null hypothesis), indicating that overall saccade latencies did not differ by age. There was a significant main effect of saccade type (initial vs. corrective saccade), $F(1, 56) = 5.9$, $p = 0.019$, $BF_{10} = 1.76$ (anecdotal evidence), indicating that initial and corrective saccade latencies differed across all age groups and blanking conditions. There was no significant main effect of blanking condition, $F(1, 28) = 2.04$, $p = 0.16$, $BF_{10} = 0.39$ (anecdotal evidence for the null hypothesis), indicating that overall latencies did not differ between blanking conditions. There was, however, a significant interaction between saccade type and age, $F(1, 56) = 14.3$, $p = 0.0004$, $BF_{10} = 87.9$ (very strong evidence), suggesting that

across both blanking conditions the difference between initial and corrective saccade latencies differs by age. Post hoc multiple comparisons with a Holm correction demonstrate a significant difference between saccade type for adults, $t(56) = -4.39$, $p = 0.0001$, but not for children, $t(56) = 0.96$, $p = 0.34$. There was no significant interaction effect between saccade type and blanking condition, $F(1, 56) = 2.66$, $p = 0.11$, $BF_{10} = 0.66$ (anecdotal evidence for the null hypothesis), or among age group, saccade type, and blanking condition, $F(1, 56) = 0.82$, $p = 0.37$; however, $BF_{10} = 9.41$ provides moderate evidence for an interaction.

To further investigate the relationship between initial and corrective saccade latencies, we calculated the log ratio of corrective saccade latency and initial saccade latency for each participant (Figure 4B). The log value was used to place ratio values below and above 1 on the same scale. We compared this log ratio between the two age groups (children and adults). A linear model showed a significant difference between the groups, $F(1, 28) = 7.22$, $p = 0.012$, $BF_{10} = 4.44$ (moderate evidence). This indicates that this ratio changed across age; relative to adults, younger participants had shorter corrective saccade latencies relative to their initial saccades. Specifically, although older adults had longer corrective than initial saccade latencies, initial and corrective saccade latencies for children did not differ. This suggests that children were faster to execute a corrective saccade compared to adults. Although on average corrective and initial saccade latencies did not differ for children, seven out of 14 children were even able to execute corrective saccades at latencies shorter than their initial saccades.

Corrective saccade latencies versus landing error

Previous studies have shown that the latency of corrective saccades depends on the magnitude of error after the initial saccades (Becker, 1972; Kapoula & Robinson, 1986; Lisi, Solomon, & Morgan, 2019; Ohl, Brandt, & Kliegl, 2011; Ohl, Brandt, & Kliegl, 2013). Hence, the shorter latencies of corrective saccades in children might be a mere consequence of their more variable landing errors in initial saccades (Figure 3; Table 1). If children have a higher predicted landing error due to more variability in saccade execution or planning, they should be faster to execute a corrective saccade to rectify this predicted error.

To test this hypothesis, we next looked at the relationship between corrective saccade latencies and horizontal landing error. For this analysis, landing error was calculated as horizontal distance between initial saccade landing position and postsaccadic stimulus position. Negative errors indicate an undershoot followed by an outward corrective saccade, and positive errors indicate an overshoot followed by an inward corrective saccade (Figure 5C).

To compare differences between children and adults, we calculated mean corrective saccade latencies separately for undershoots and overshoots of initial saccades, corresponding to outward or inward corrective saccades, respectively (Figure 5, diagram; gray panels). For each blanking condition, we compared groups using a linear mixed model with fixed effect of age group (adults or children) and initial saccade error direction (undershoot or overshoot), and random intercepts for participant. For the no-blank condition, there was a significant effect of age group, $F(1, 28) = 15.96$, $p = 0.0004$; $BF_{10} = 42.9$ (very strong evidence), and initial saccade error direction, $F(1, 27) = 13.63$, $p = 0.001$, $BF_{10} = 15.85$ (strong evidence), as well as a significant interaction between age group and initial saccade error direction, $F(1, 27) = 8.66$, $p = 0.0066$, $BF_{10} = 4.9$ (moderate evidence). Post hoc multiple comparisons with a Holm correction showed a significant difference between undershoots and overshoots for children, $t(27) = 4.64$, $p = 0.0002$, but not for adults, $t(27) = 0.54$, $p = 0.59$. For the blank condition, there was a significant effect of age group, $F(1, 28) = 8.07$, $p = 0.0083$, $BF_{10} = 3.79$ (moderate evidence), but not of initial saccade error direction, $F(1, 28) = 3.31$, $p = 0.08$, $BF_{10} = 1.17$ (anecdotal evidence), or interaction between age group and initial saccade error direction, $F(1, 28) = 0.016$, $p = 0.9$, $BF_{10} = 0.32$ (moderate evidence for the null hypothesis). These results suggest that children made faster corrective saccades than adults for undershoots rather than overshoots, but this only seemed to occur in the no-blank condition. We outline potential explanations for this difference in the Discussion section.

Discussion

This study investigated how blanking affects SSD in children 7 to 12 years of age and adults. The results showed that in the no-blank condition children had overall larger JNDs than adults (i.e., greater SSD). Children also showed a larger blanking effect (improvement in JND from the no-blank to the blank condition) than adults. Measures of saccade dynamics show that initial saccades were more variable and had a larger undershoot in children. At the same time, children had shorter corrective saccade latencies than adults, especially when the initial saccade undershoots the postsaccadic target. Taken together, these results suggest that, compared to adults, children tolerate larger intrasaccadic displacements, thereby perceiving the stimulus as stationary. This may be due to a greater internal expectation or prediction of any discrepancy between pre- and postsaccadic location information

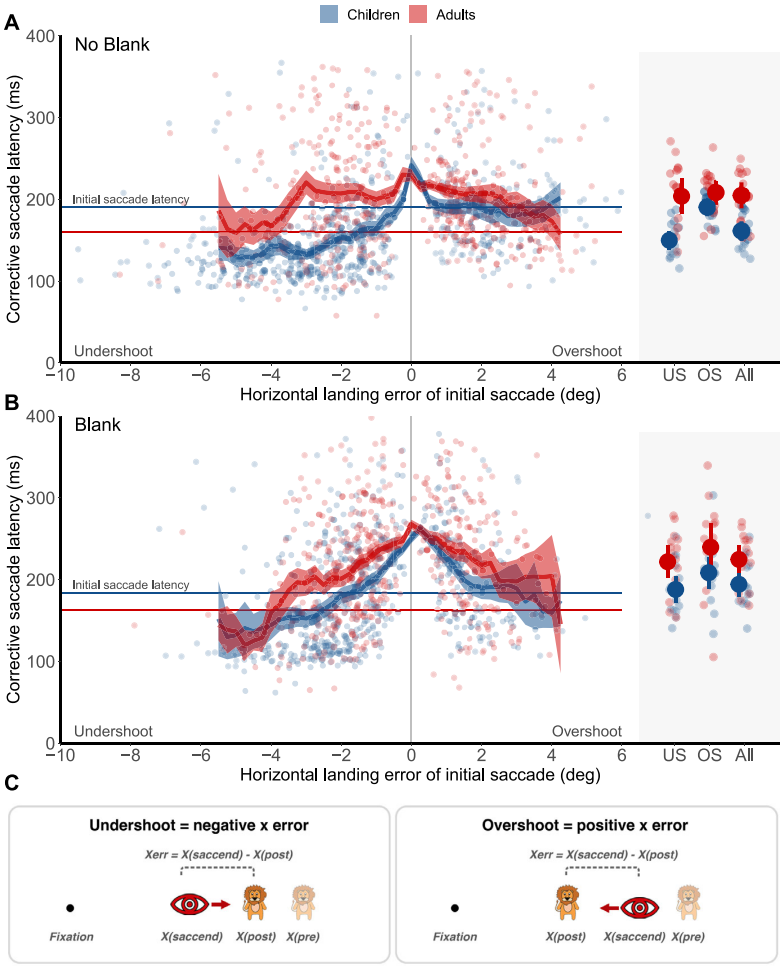

Figure 5. Landing error (initial saccade endpoint to postsaccadic stimulus) versus corrective saccade latency for no-blank trials (A) or blank trials (B). Points in the white panels are individual saccade latencies for all subjects; ribbon plots represent a moving average of saccade latencies for all participants across the range of landing errors (average latencies were calculated in a moving window ranging from –5.75 to 4.25 in steps of 0.25°, with a window size of 0.5°). Small symbols in the gray panels indicate mean saccade latencies for individual subjects grouped by undershoot (US) or overshoot (OS), or both (All); large symbols represent mean saccade latencies across all participants. All error bars are 95% CIs. Adults are represented with red markers, children with blue. (C) Examples to illustrate *x*-axis landing error calculation for corrective saccades for undershoots and overshoots, showing the pre- and postsaccadic positions of the stimulus, initial saccade landing position, and direction of the corrective saccade (red arrow).

being self-induced due to greater or more variable motor error or target localization error.

SSD and greater movement variability in children

Perhaps the most parsimonious explanation for why children showed greater SSD than adults is that they have a larger uncertainty about their saccade landing position relative to the target (saccadic uncertainty). The models of Niemeier et al. (2003) and Atsma et al. (2016) both predict that stronger SSD is due to increased internally caused uncertainty. A larger saccadic uncertainty in children may result in a larger tolerance for intrasaccadic position changes (Niemeier et al., 2003). This is evidenced by two factors in our data: children had more variable initial saccade landing errors and faster corrective saccade latencies. Variability

in saccade gain decreases with age (Bucci & Seassau, 2012; Munoz et al., 1998; Salman et al., 2006), and we saw that the children in this study also had greater horizontal landing variability than the adult group (Figure 3). Wexler and Collins (2014) suggested that there is an elliptical zone around the saccade endpoint in which stimulus displacements are not noticed; this region reflects the variance of saccade landing positions. Given that children have more variability in horizontal landing error, they may be more likely to have a larger "window" of tolerance for intrasaccadic displacements. In terms of SSD, this means that larger displacements will be tolerated than in adults, who have smaller variability in saccade landing error.

The second line of evidence comes from faster corrective saccades in children. If children have a higher internal expectation or prediction of an inaccurate saccade, they should be faster to execute a corrective saccade to account for this predicted error. Note that expectation in this sense is not a conscious expectation but rather an internal prediction of greater motor error by the oculomotor system. As Figure 4 shows, children are faster to execute corrective saccades than adults even at similar error sizes, and this is especially the case when the corrective saccade is made to correct an undershoot of the initial saccade. Saccades are typically hypometric (Becker, 1989), and this is also the case in children, although children additionally have greater variability in their saccade gain (Munoz et al., 1998; Salman et al., 2006) (and see Figure 3). In trials where the initial saccade undershoots both the pre- and postsaccadic stimulus location (Figure 5C), there could be a high internal expectation for the discrepancy between landing position and target location, as this would automatically be attributed to the natural high variability in saccade undershoot. Hence, a corrective saccade is rapidly executed. In the case where the initial saccade overshoots the postsaccadic target position, the discrepancy in pre- and postsaccadic stimulus location may be less expected (as saccade overshoots are less common), thus corrective saccade latencies are slower. Interestingly, this effect is more prominent in the no-blank condition. This may be due to the fact that, in the no-blank condition, the anticipated corrective saccade can be executed immediately as the postsaccadic target information is available upon landing, whereas in the blank condition the target is not available directly after the saccade (Tian, Ying, & Zee, 2013). The corrective saccades in the blank condition are more likely to be reactive saccades in response to the reappearing target, which are independent from the high expectation of having to correct an inaccurate initial saccade.

Shorter corrective saccade latencies and greater landing variability in children seem to suggest that children are more variable in their saccade execution and have a greater internal expectation of saccadic error. This would adhere to the framework of Atsma et al. (2016) and Niemeier et al. (2003) regarding greater SSD being caused by increased intrinsic uncertainty. Although Atsma et al. (2016) considered localization uncertainty to be one potential source of uncertainty, Niemeier et al. (2003) referred to saccade landing variability. While they ostensibly refer to different processes, it is possible that saccade landing variability inherently reflects the inability to localize the peripheral target accurately (Lisi et al., 2019). It has been suggested that the major component causing saccade landing variability is uncertainty in peripheral target localization and that noise in motor commands explains only a small fraction of the variability (van Beers, 2007), however that study focused on adults, and the relative contribution of motor noise may be higher in children with a less well-calibrated oculomotor system. We cannot dissociate whether, in this current study, the variability in landing position for children came from more noise in motor execution compared to adults or was due to greater uncertainty in peripheral target localization. Different parameters associated with saccade execution develop at different times. Peak velocity and accuracy develop faster than saccade latencies and fixation control (Munoz et al., 1998; Salman et al., 2006), suggesting that structures controlling saccade execution located in the brainstem and cerebellum (Leigh & Zee, 1991; Wurtz & Goldberg, 1989) may develop earlier than cortical structures controlling saccade programming in the parietal and frontal networks, as frontal regions do not reach maturity until late adolescence (Anokhin, Birbaumer, Lutzenberger, Nikolaev, & Vogel, 1996; Thatcher, Walker, & Giudice, 1987). This may point to increased uncertainty in localization in children compared to adults, but we cannot confidently make any conclusions based on the current data.

While the assumption of greater internal uncertainty in saccade planning may be our favored hypothesis to explain these results, there are a number of other, non-mutually exclusive potential explanations. One mechanism related to SSD is saccadic suppression of contrast sensitivity, and children have been shown to have over three times greater saccadic suppression of contrast sensitivity than adults (Bruno et al., 2006). Our observed results of greater SSD in children could be due to greater suppression in general during the saccade.

Furthermore, increased SSD in children could also be due to temporal factors. Research suggests that there is a specific postsaccadic spatiotemporal window where the system determines whether stimuli surrounding the saccade endpoint are the same as the presaccadic stimuli (Deubel et al., 1998). It could therefore also be the case that this temporal window is widened, due to greater uncertainty about when they are executing a saccade. If children are unable to segregate stimulus information

into pre- or postsaccadic categories, they would not be able to accurately calculate intrasaccadic position changes; however, we think that this explanation is less likely, as a number of studies suggest that temporal integration windows in children do not differ from adults (Arnett & di Lollo, 1979; Hogben, Rodino, Clark, & Pratt, 1995) and, more importantly, that children are also able to segment temporal information as well as adults by the age of 5 (Freschl, Melcher, Kaldy, & Blaser, 2019).

An alternative explanation for larger JNDs in children is that children might have more unintentional errors or a greater fluctuation in attention rather than stronger SSD. Although it is probable that children's data are inherently more noisy than those of adults, we would expect that this would affect blank and no-blank conditions alike, resulting in a similar blanking effect as in adults. This is supported by the observation that the quality of the psychometric function fits was similar in the blank and the no-blank condition. Therefore, we think it is unlikely that the difference in SSD and the blanking effect between children and adults is caused by inattention in children.

Blanking effect and the development of integration in children

In this study, we observed that introducing a blank between the pre- and postsaccadic stimulus reduced SSD, and this blanking effect was even larger for children than for adults. These results provide an insight into how mechanisms of integration and segregation may develop in children. The increased SSD for children suggests that unisensory integration mechanisms may be developed in even the youngest participants (7 years old). Although this may at first glance be in contradiction with studies of the development of multisensory integration which suggest that *less* integration occurs due to an ongoing perceptual and oculomotor calibration process (Ernst, 2008; Gori et al., 2008), the same underlying principle could apply. Here, we saw that children showed more SSD, so potentially more integration of pre- and postsaccadic position information than adults. We can speculate that children are still calibrating how discrepancies in pre- and postsaccadic position error relate to their own saccadic accuracy, and the narrowing spatial window of integration with age reflects this ongoing calibration process. This calibration process may be crucial for the visual system to learn its own motor errors; as the visuomotor system develops, it must learn when transsaccadic position changes can be attributed to either internal factors (i.e., motor error or localization uncertainty) or external factors, such as a physical position change. If position discrepancies are falsely attributed to external factors early in development, then the oculomotor system would never learn its own errors. If it assumes (as may be evident from this study) more error from its own noisy localization and execution, it can learn to correct these errors.

Indeed, feedback has been shown to be vital in the development of sensory integration and calibration; children can learn to integrate sensory cues only when they receive feedback about their judgments (Negen et al., 2019), and delaying feedback inhibits sensorimotor recalibration in children (Vercillo, Burr, Sandini, & Gori, 2015). Also, and in comparison to the multisensory development literature, many studies have shown that the ability to integrate and segment basic visual features, motion, and patterns develops very early in life (for review, see Braddick & Atkinson, 2011). This multi-stage development of integration mechanisms may reflect both the complexity of the information being integrated and ongoing physical development. It may be unsurprising that basic visual feature integration develops early, as the basic architecture of the visual system matures within the first few years of life (Braddick & Atkinson, 2011). Integration of different visual features such as stereo and motion or texture, which has been found to occur in adults (Johnston, Cumming, & Landy, 1994; Knill & Saunders, 2003), may be slower to develop, as depth processing is calibrated to account for the changing position of the eyes in a growing head, in a manner similar to how integration of visuohaptic information relies on the calibration of the developing haptic system (Ernst, 2008; Gori et al., 2008). Adults can learn novel cue combination within a few hours (Negen, Wen, Thaler, & Nardini, 2018), suggesting that the slow development of multisensory cue combination may be limited by biological development (Negen et al., 2019).

A caveat to this discussion, however, is that we cannot say for certain whether increased SSD is caused by an increase in integration per se or whether it is rather a failure to segregate. While models such as those posited by Atsma et al. (2016) and Niemeier et al. (2003) may predict a dichotomous relationship between integration and segregation, this may be an oversimplification of a more nuanced set of processes, and the finding that children do not segregate pre- and postsaccadic information does not mean that they necessarily integrate it. As such, and while this study provides insight into the development of SSD and transsaccadic location integration, we are hesitant to draw conclusions about the generalizability of these results to other potentially related measures of transsaccadic integration. It may be the case that these results do reflect a well-developed transsaccadic integration mechanism in children, and this may extend to integration of feature information such as orientation and color, as well as location information. Whether this integration would be near-optimal, as it is

in adults (Ganmor et al., 2015; Wolf & Schütz, 2015), is unclear. A likely scenario is that integration occurs; however, as with multisensory integration (Ernst, 2008; Gori et al., 2008), until the calibration of oculomotor systems is complete this integration may be suboptimal.

In children, as in adults, the intervening blank decreased SSD. The Atsma et al. (2016), and Niemeier et al. (2003) models predict that, when a blank is introduced, the stimuli should be segregated rather than integrated; the decreased JNDs in the blank condition compared to no-blank condition for both children and adults are in accordance with this hypothesis. The introduction of a blank provides an additional cue that the intrasaccadic position change may be due to a change in the environment. When the world is no longer assumed to be stable, any discrepancies between pre- and postsaccadic positions can be attributed to a change in the world, rather than internal uncertainty (Niemeier et al., 2003). These results also suggest that the assumption of a stable visual world may have developed by the age of 7, which may not be surprising, as this is a core mechanism underpinning transsaccadic perceptual stability.

It should also be noted that the magnitude of the blanking effect observed in this study was relatively small for adults compared to some previous studies (Table A3). One possible explanation is that the blanking effect has been shown to decrease with decreasing luminance contrast and for isoluminant color (Matsumiya et al., 2016; Takano et al., 2020), and, although our stimuli are far from low luminance contrast, the small blanking effect for adults might be explained by the strong color contrast in our stimuli, which were designed primarily to be appealing to children. Interestingly, these results are similar to those of Tas et al. (2012), who found a smaller blanking effect for colored, real-world stimuli compared to the typically utilized monochrome black disk stimulus (Table A3). While investigating the role of stimulus properties on blanking was not a goal of this study, it is interesting to note that these results, taken together with those of Tas et al. (2012), indicate that the blanking effect may be reduced for colorful, complex stimuli.

Initial saccade latencies

In accordance with previous studies, initial saccade latencies were shorter for adults than children; however, the initial saccade latencies for children in this study are considerably shorter than those previously reported (Table A4). This could be due to discrepancies in the stimuli used; while previous studies utilized a monochrome point or square target, our targets were specifically designed to be interesting for children and were embedded in an exciting narrative. Cohen & Ross (1977, 1978) found that when children were given a "warning" signal 300 ms before the saccade, saccade latencies reflected those of adults, suggesting that processing limitations are not necessarily the cause of longer latencies in children, and higher level factors could be responsible instead. In adults, it has been shown that saccade latencies can be reduced by about 35 ms if the saccade target is associated with a perceptual task (Bieg, Bresciani, Bülthoff, & Chuang, 2012; Guyader, Malsert, & Marendaz, 2010; Montagnini & Chelazzi, 2005; Trottier & Pratt, 2005; Wolf & Schütz, 2017). It is possible that the saccade latencies in children may depend more on motivational aspects and that their facilitation by an engaging task is even larger than in adults. Because our task was designed to be especially motivating for the children, we can be sure that our young participants were paying attention to the task. The remaining delay in initial saccade latency compared to adults might be due to increased localization uncertainty, which may result in a longer processing time (Carpenter, 2004; Collins, 2016; van Loon & Adam, 2006; Zimmermann et al., 2013); this would be in accordance with the increased intrinsic uncertainty assumption.

Postsaccadic presentation duration

One noteworthy methodological difference between this and previous studies on SSD and blanking effects concerns the presentation duration of the postsaccadic target. While we used a fixed presentation duration of 400 ms for the postsaccadic stimulus, all other studies listed in Table A3 varied the duration depending on participant response time, which is presumably in the range of 500 to 1000 ms after saccade landing. Hence, it can be assumed that we provided less time for encoding the postsaccadic target location compared to previous studies, and one might argue that this affected the strength of SSD. However, we think that this was not the case for two reasons. First, the postsaccadic target duration was sufficiently long to allow for the execution of corrective saccades that were directed at the new postsaccadic location of the target (Figure A3); hence, the information about the new postsaccadic target location was already available and processed in the oculomotor system. Second, the mean JNDs of adults in the no-blank condition were well within the range of reports in the literature, suggesting that our paradigm produced typical SSD.

Conclusions

This study showed that children 7 to 12 years old experience greater saccadic suppression of displacement than adults and additionally show a greater blanking effect than adults. Children had larger undershoots and

more variability in their initial saccades than adults and were faster to execute corrective saccades in response to these undershoots. Taken together, these results suggest that children have a greater expectation for inaccurate saccades and therefore have greater tolerance for discrepancies in pre- and postsaccadic stimulus position.

Keywords: saccade, transsaccadic, children, blanking, saccadic suppression of displacement

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Appendix

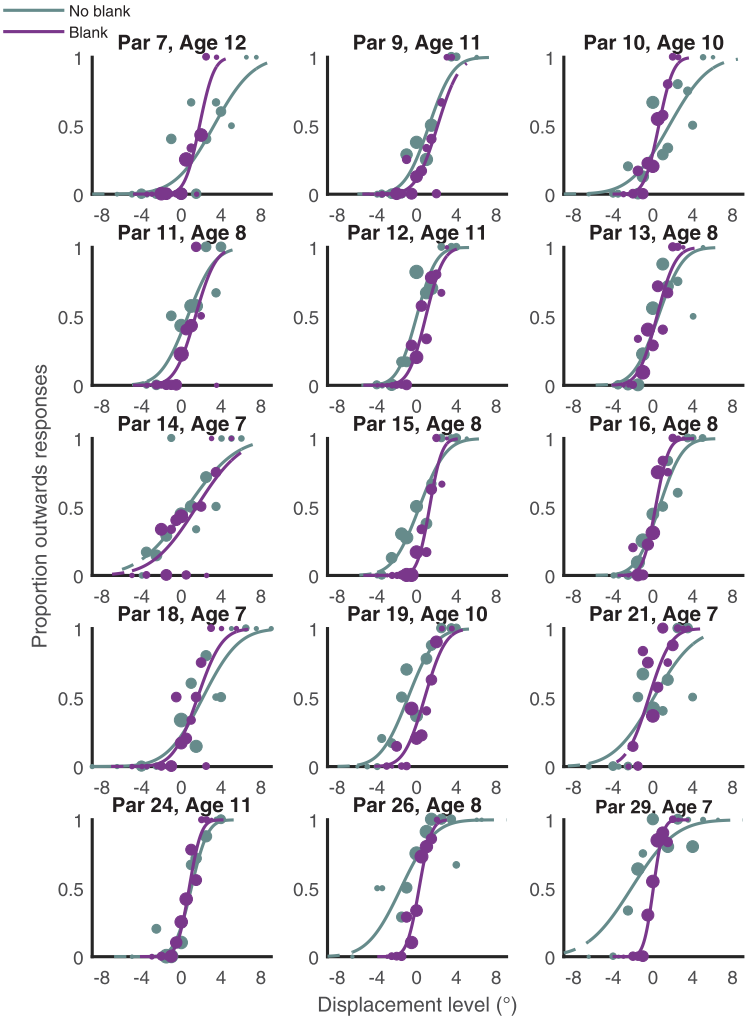

Figure A1. Psychometric functions for all children showing fitted cumulative Gaussian distributions for blank (purple) and no-blank (turquoise) conditions.

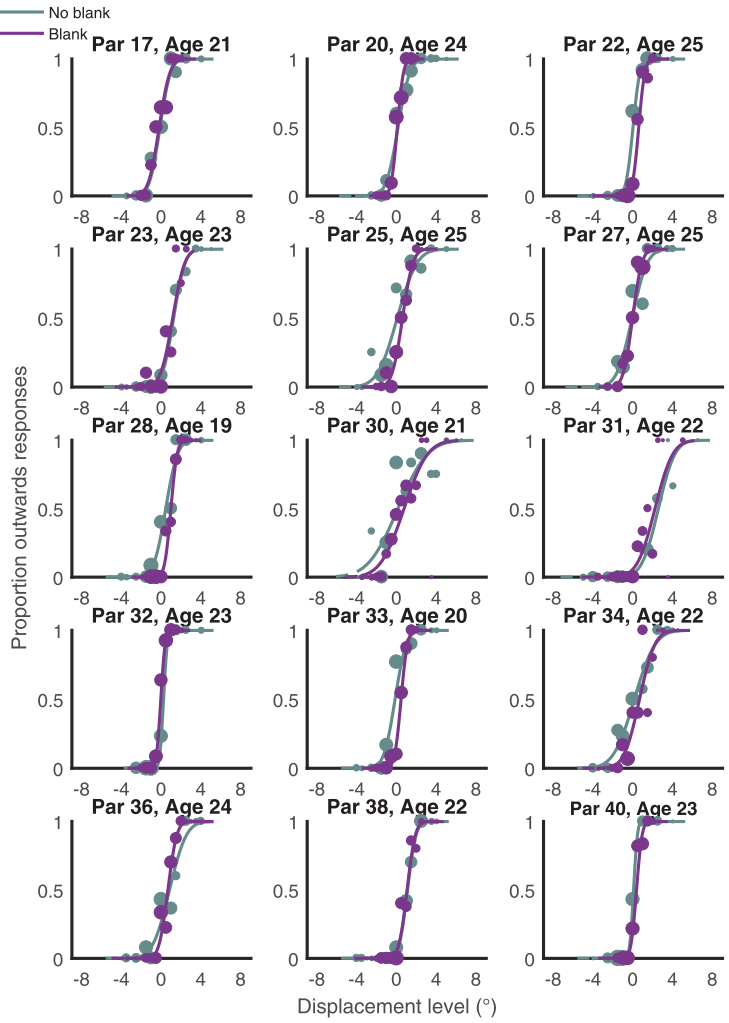

Figure A2. Psychometric functions for all adults showing fitted cumulative Gaussian distributions for blank (purple) and no-blank (turquoise) conditions.

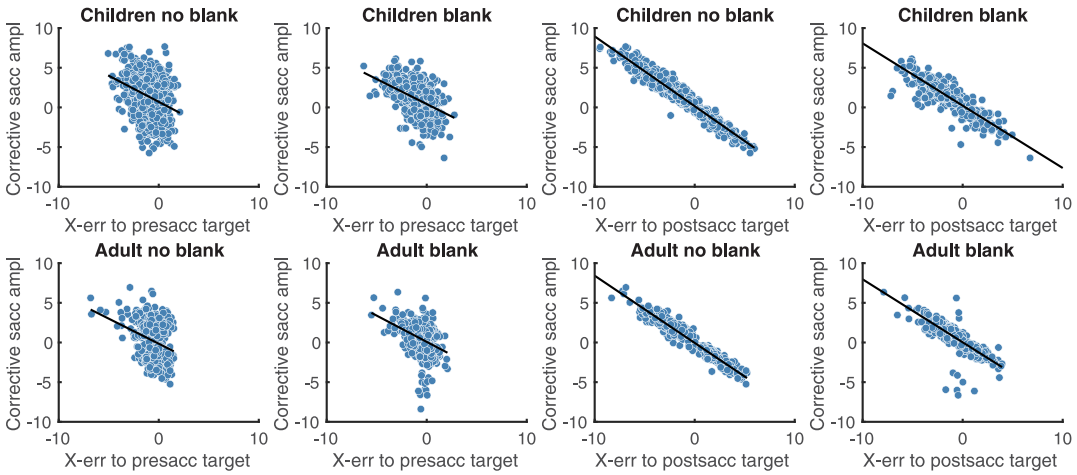

Figure A3. Correlation between corrective saccade amplitude and horizontal landing error to pre- or postsaccadic target position. Correlation coefficients for amplitude versus presaccadic target position: children no-blank, –0.33; children blank, –0.46; adult no-blank, –0.31; adult blank, –0.38. Correlation coefficients for amplitude versus postsaccadic target position: children no-blank, –0.97; children blank, –0.89; adult no-blank, –0.97; adult blank, –0.84.

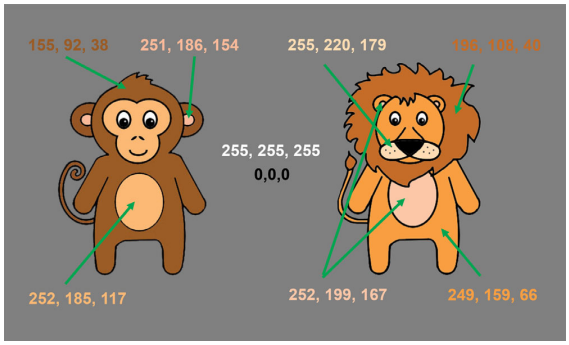

Figure A4. Lion and monkey stimuli with RGB values on a gray (128, 128, 128) background.

						Mean (SD)		
Child participant number	Age (y)	Erroneous saccades (*n*)	Saccade latency	Total number of exclusions	Total number of valid trials; total number of trials	Number of trials per displacement level in no-blank condition	Number of trials per displacement level in blank condition	Normalized deviance no-blank; blank
7	12	22	18	40	104; 144	3.63 (1.96)	3.54 (2.79)	0.89; 0.37
9	11	27	0	27	117; 144	4.67 (2.5)	3.81 (2.4)	0.49; 0.71
10	10	11	0	11	133; 144	4.64 (2.53)	5.67 (3.28)	0.93; 0.42
11	8	32	20	52	92; 144	4.5 (1.84)	3.92 (2.39)	0.7; 1.05
12	11	11	3	14	130; 144	5.91 (3.18)	4.33 (3.04)	0.71; 0.39
13	8	11	12	23	121; 144	5.36 (3.11)	4.77 (3.3)	1.06; 0.6
14	7	37	0	37	107; 144	4.77 (2.62)	3.21 (2.01)	0.87; 0.75
15	8	7	9	16	152; 168	6.08 (3.32)	5.64 (4.33)	0.47; 0.5
16	8	21	5	26	142; 168	5.67 (3.37)	6.17 (4.11)	0.38; 0.75
18	7	37	36	73	95; 168	2.94 (2.46)	2.65 (1.73)	0.51; 0.64
19	10	11	0	11	157; 168	6.23 (3.03)	5.85 (3.67)	0.67; 0.78
21	7	13	14	27	141; 168	5.75 (2.86)	5.54 (2.82)	1.48; 1.44
24	11	18	3	21	147; 168	6.7 (3.65)	6.67 (4.21)	1; 0.45
26	8	17	10	27	141; 168	5.14 (3.98)	6.27 (3.5)	0.99; 0.42
29	7	20	0	20	148; 168	5.36 (3.77)	6.64 (4.08)	1.09; 0.47
Mean (SD)	9 (2)	20 (10)	9(10)	28 (17)	128 (21)	5.16 (1.0)	4.98 (1.32)	0.82 (0.29); 0.65 (0.34)

Table A1. Trial exclusions for children.

						Mean (SD)		
Adult participant number	Age (y)	Erroneous saccades (*n*)	Saccade latency	Total number of exclusions	Total number of valid trials; total number of trials	Number of trials per displacement level in no-blank condition	Number of trials per displacement level in blank condition	Normalized deviance no-blank; blank
17	21	2	0	2	166; 168	9.22 (4.47)	7.55 (4.55)	0.75; 0.51
20	24	6	11	17	151; 168	6.25 (4.37)	8.44 (4.3)	0.19; 0.29
22	25	15	4	19	149; 168	6.91 (5.11)	6.64 (4.82)	0.22; 0.31
23	23	2	0	2	166; 168	6.92 (4.62)	6.92 (4.08)	0.1; 1.32
25	25	8	12	20	148; 168	6.17 (4.28)	6.17 (4.15)	0.52; 0.34
27	25	21	1	22	146; 168	6.5 (4.6)	6.18 (4.47)	0.58; 0.23
28	19	40	4	44	124; 168	5.73 (3.72)	5.55 (3.62)	0.4; 0.18
30	21	7	1	8	160; 168	5.57 (4.38)	5.13 (3.59)	1.31; 0.7
31	22	8	0	8	160; 168	6.08 (3.8)	5.06 (3.45)	0.2; 0.8
32	23	9	4	13	155; 168	10 (5.13)	7.5 (4.43)	0.03; 0.05
33	20	19	1	20	148; 168	6.82 (4.42)	6.64 (4.01)	0.47; 0.16
34	22	1	0	1	167; 168	7.64 (4.15)	5.53 (4.61)	0.37; 0.92
36	24	14	6	20	148; 168	7.18 (4.33)	4.93 (3.97)	0.67; 0.32
38	22	3	1	4	164; 168	7.27 (4.41)	6.46 (4.59)	0.07; 0.45
40	23	0	0	0	168; 168	9.33 (6.56)	8.4 (5.36)	0.02; 0.41
Mean (SD)	23 (2)	10 (10)	3 (4)	13 (12)	155 (12)	7.17 (1.35)	6.47 (1.14)	0.39 (0.35); 0.47 (0.29)

Table A2. Trial exclusions for adults.

	Stimulus				JNDs (°)		Blanking effect			
Reference	Type	Size (°)	Eccentricity (°)	Blank duration (ms)	No-blank	Blank	Relative	Absolute (°)	Postsaccadic duration (ms)	Sample size (*n*)
Deubel et al. (1996)	Cross	0.2	6 or 8	250	1.00	0.50	0.67	0.50	Until response (∼500–1000 ms)	6
Ostendorf et al. (2010)	Cross	0.5	6 or 8	250	1.18	0.51	0.79	0.67	Until response (maximum 5 s)	8
Irwin & Robinson (2018)	Cross	0.8	6 or 8	300	2.07	0.87	0.82	1.20	Until response	12
Tas et al. (2012)	Dot	0.33	6 to 8	250	0.85	0.49	0.54	0.36	Until response	7
Tas et al. (2012)	Circular objects	0.65	6 to 8	250	0.97	0.72	0.30	0.25	Until response	7
This study (children)	Cartoon animal	2.39 × 1.76; 2.51 × 1.72	8 or 10	300	2.48	1.46	0.52	1.02	400	15
This study (adults)	Cartoon animal	2.39 × 1.76; 2.51 × 1.72	8 or 10	300	1.05	0.80	0.24	0.25	400	15

Table A3. Blanking effect and parameter comparison to previous studies.

Study	Initial saccade latency (ms)	Age (y)	Target amplitude (°)	Paradigm	Sample size per group (*n*)
This study, mean (SD)	186.4 (129) 162.1 (79.9)	7–12 19–25	8 or 10	Overlap paradigm	15
Cohen & Ross (1977)	∼273 ∼218	Mean 8.7 Unspecified adult	15 L/R	No warning signal	10
Cohen & Ross (1978)	∼258 ∼223	Mean 8.5 Mean 23.7	10 L/R	No warning signal	10
Munoz et al. (1998)	∼325 ∼250	9 23	20 L/R	Overlap paradigm	∼16
Salman et al. (2006), mean (SD)	248.7 (20.5) 253.6 (27.4)	8–19 —	10 R 10 L	—	39
Bucci & Seassau (2012)	∼300	9	15 L/R	Overlap paradigm	16

Table A4. Comparison of children and adult saccade latencies between this study and past studies. Where exact values were not provided in previous studies, we have approximated values from the published figures, at mean ages comparable to the ages tested in this study.

Amended February 24, 2021: A couple of minor typos were corrected, and the faint box around the monkey image in Figure 1A was removed.

Study III

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A bias in saccadic suppression of shape change

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ABSTRACT

Processing of visual information in the central (foveal) and peripheral visual field is vastly different. To achieve a homogeneous representation of the visual world across eye movements, the visual system needs to compensate for these differences. By introducing subtle changes between peripheral and foveal inputs across saccades, one can test this compensation. We morphed shapes between a triangle and a circle and presented two different change directions (circularity decrease or increase) at varying magnitudes across a saccade. In a change-discrimination task, observers disproportionally often reported percepts of circularity increase. To test the relationship with visual-field differences, we measured perception when shapes were exclusively presented either in the periphery (before a saccade), or in the fovea (after a saccade). We found that overall shapes were perceived as more circular before than after a saccade and the more pronounced this difference was for a participant, the smaller was their circularity-increase bias in the change-discrimination task. We propose that visual-field differences have a direct and an indirect influence on transsaccadic perception of shape change. The direct influence is based on the distinct appearance of shape in the central and peripheral visual field in a trial, causing an increase of the perceptual magnitude of circularity-decrease changes. The indirect influence is based on long-term build-up of transsaccadic expectations; if a change is opposite (circularity increase) to the expectation (circularity decrease), it should elicit a strong error signal facilitating change detection. We discuss the concept of transsaccadic expectations and theoretical implications for transsaccadic perception of other feature changes.

1. Introduction

The human visual system achieves a high visual resolution and a large field of view despite limitations in processing. The centre of the visual field, namely the fovea, provides highly detailed and relatively undistorted information due to the high density of cone photoreceptors (Oesterberg, 1935; Curcio et al., 1990) and an overrepresentation in the visual cortex (e.g., Dow et al., 1981; Azzopardi & Cowey, 1993; Dumoulin & Wandell, 2008). The periphery provides a large field of view, albeit with less detailed and more spatially distorted information (for reviews, see Strasburger et al., 2011; Rosenholtz, 2016). One function of saccades is to bring relevant objects into the fovea, which inevitably leads to a drastic change in the incoming low-level information due to this physiological disparity between foveal and peripheral processing. Given that human perception appears to be homogeneous and stable across eye movements, there must exist a mechanism eliminating such self-induced differences between pre- and postsaccadic information and previous research revealed a number of behavioural observations that might be the result of such a compensation mechanism.

One line of research reports relatively poor performance when externally induced visual changes at the moment of a saccadic eye movement have to be detected. This phenomenon is generally referred to as saccadic suppression and applies to a number of visual object properties such as spatial position (saccadic suppression of displacement, e.g., Bridgeman et al., 1975), object contour (Henderson, 1997; Demeyer et al., 2010), orientation (Henderson & Hollingworth, 1999; De Graef & Verfaillie, 2002; Grzeczkowski et al., 2020), object type and token (Henderson & Hollingworth, 2003), luminance (Henderson et al., 2008), and spatial frequency (Weiß et al., 2015). This elevation of change-detection thresholds during a saccade compared to fixation has been interpreted in the sense that the visual system has a tendency to discard small intrasaccadic changes and instead to maintain the assumption of a stable external world (e.g., MacKay, 1972). A prior assumption of external stability might hence be one measure by the visual system to compensate for self-induced discrepancies such as due

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to visual-field differences. Interestingly, saccadic suppression of change detection is not inevitable as accompanying signals can facilitate intrasaccadic change detection such as target blanking (e.g., Deubel et al., 1996; 2002), changes in image size (McConkie & Currie, 1996), form changes (Demeyer et al., 2010), orthogonal target displacements (Wexler & Collins, 2014), and luminance or surface feature changes (Tas et al., 2012). Such visual events may break the stability assumption; but this and alternative explanations for their facilitative effect are still debated (e.g. Tas et al., 2012; Ziesche et al., 2017; Born, 2019) because a comprehensive charactarisation of the circumstances that lead to the facilitation is still missing.

Another line of research suggests that differences across the visual field are accounted for by the means of transsaccadic learning and transsaccadic predictions. Specifically, it has been shown that presaccadic stimuli appear more alike to a consistently accompanying postsaccadic stimulus after a relatively brief learning phase (e.g., Cox et al., 2005; Herwig & Schneider, 2014; Valsecchi & Gegenfurtner, 2016; for a review see Stewart, Valsecchi, & Schütz, 2020). Consistent with predictive coding theory (e.g., Rao & Ballard, 1999; Friston, 2009; for a review see de Lange et al., 2018), it has been suggested that a visual signal (Edwards et al., 2017), based on the recent transsaccadic experience, is generated upon processing of the presaccadic input and integrated with it leading to the biased appearance of the presaccadic stimulus. In essence, this line of research also suggests an experience-based mechanism (as any prediction should be based on experience) and this more specified predictive-coding mechanism might be likely candidates for how the visual system compensates for self-induced discrepancies and might as well be at the basis of intrasaccadic change detection (Ehinger et al., 2015).

To further characterise transsaccadic perception of change as well as to understand its relationship with appearance differences across the visual field, we investigated transsaccadic change perception a) of a key feature to mediate object constancy referred to as shape, form, or contour curvature (Kayaert et al., 2003; El-Shamayleh & Pasupathy, 2016), and b) with or without an accompanying signal that is known to facilitate change detection: a postsaccadic blank (Deubel et al., 1996). Additionally, we tested shape appearance pre- and postsaccadically, i.e., in the peripheral and central visual field. It is known from previous literature that the shape of geometric objects is perceived differently in the fovea and periphery (Baldwin et al., 2016; Coates et al., 2017; Valsecchi et al., 2018). Differences in appearance could have a direct effect on change perception as they could either perceptually increase or decrease the magnitude of a given physical discrepancy between pre- and postsaccadic inputs. For example, if shape is generally perceived as more circular in the periphery than in the fovea, intrasaccadic changes that increase circularity across a saccade should be reduced in perceived magnitude. Another and more indirect influence may come from transsaccadic predictions that are based on experienced transsaccadic contingencies. For example, in a scenario in which a less circular shape is predicted to follow after a saccade, a prediction error should be larger for more circular postsaccadic shapes and changes may be detected more easily.

2. Methods

The goal of this study was to investigate perception of shape changes across saccades and its interaction with perceptual differences between the peripheral and the foveal visual field. A second experiment was conducted to narrow down possible explanations for the direction of the observed bias in Experiment 1. Both experiments were divided into two parts: part A investigated transsaccadic shape change perception, and part B pre- (peripheral) and postsaccadic (foveal) shape appearance.

2.1. Participants

In Experiment 1, we tested 18 participants who were unaware of the purpose of the study of which one had to be excluded for not having executed a saccade in 98% of trials in part B. The data of 17 participants (10 females, 7 males; mean age = 23 years, range = 21–25 years) was used for analysis. In Experiment 2, a different group of 18 participants, who were unaware of the purpose of the study, was tested. Five of these participants had to be excluded. One did not complete both experimental parts. The four other excluded participants showed detection thresholds (in part A) that were unreasonably high (outside of our measurement range). That means that those participants did not achieve 75%-correct responses in at least one condition even with the largest shape changes we could apply. Thirteen participants (9 females, 4 males; mean age = 24 years, range = 20–28 years) remained for analysis. All participants were students of Marburg University, had normal or corrected-to-normal vision, and gave informed consent prior participation. The study was conducted in accordance with the principles of the Declaration of Helsinki (1964) and authorized by the local ethics committee of the psychology department at Marburg University (proposal number 2015–35 k).

2.2. Stimuli

The presaccadic fixation stimulus in Experiment 1 and the pre- and postsaccadic fixation stimuli in Experiment 2 were a combination of a bull's-eye and crosshair (Thaler et al., 2013) with a diameter of 0.6° of visual angle, and of colour chosen randomly out of an array of colours generated in DKL colour-space (Derrington et al., 1984), with randomised polarity and isoluminance towards the grey background. The postsaccadic fixation stimulus in Experiment 1 was a black disk of 0.15° in diameter. Shape stimuli as depicted in Fig. 1A and Fig. 2A were similar to the ones used by Herwig et al. (2015) and Paeye et al. (2018), and were generated based on an equilateral triangle which sides increased in curvature k in discrete steps of 0.1 going from k = 0 (full triangle) to k = 1 (full circle). Curvature k corresponds to the ratio of the circumradius and the radius of the three circles used for the geometrical construction of a Reuleaux triangle (Reuleaux, 1875). The circumradii of the shapes (k = 0, k = 0.1, …, k = 1) in Experiment 1 were 1.72°, 1.58°, 1.46°, 1.38°, 1.31°, 1.25°, 1.21°, 1.18°, 1.15°, 1.13°, 1.11° respectively. This was done to keep the area covered by each figure approximately the same for all shapes at 5885 pixels (Fig. 1A). In Experiment 2, all shape stimuli had a circumradius of 1.28° (Fig. 2A). All shape stimuli were dark grey (RGB: 56, 56, 56).

2.3. Design

Two experiments with two parts each were conducted in this study. In both experiments, intrasaccadic change detection was measured in part A and differences between pre- and postsaccadic appearance in part B. The crucial difference between Experiment 1 and 2 was that in Experiment 1, only one stimulus was shown before and after a saccade and that participants had to discriminate the direction of the intrasaccadic shape change (stimulus became more circular or more triangular) in part A. In Experiment 2, a pair of stimuli was shown before and after a saccade and participants had to discriminate which of the two stimuli changed its shape during the saccade in part A. In part B of both experiments, participants had to judge whether a shape perceived pre- or postsaccadically was either more circular or more triangular than the mean shape across all stimuli seen throughout the experiment (method of single stimuli; Morgan et al., 2000) independently of the number of shape stimuli presented in a trial. We used a staircase procedure in part A and the method of single stimuli in part B of both experiments. In Experiment 1A, two staircases were assigned to each change direction and blanking condition. One staircase started with the smallest possible change magnitude of 0.1 $|\Delta k|$ and the other with the largest possible change magnitude of 1 $|\Delta k|$. The presaccadic shape was chosen randomly amongst all shapes that were not too close to the end of the shape range in respect to the applied change magnitude and direction.

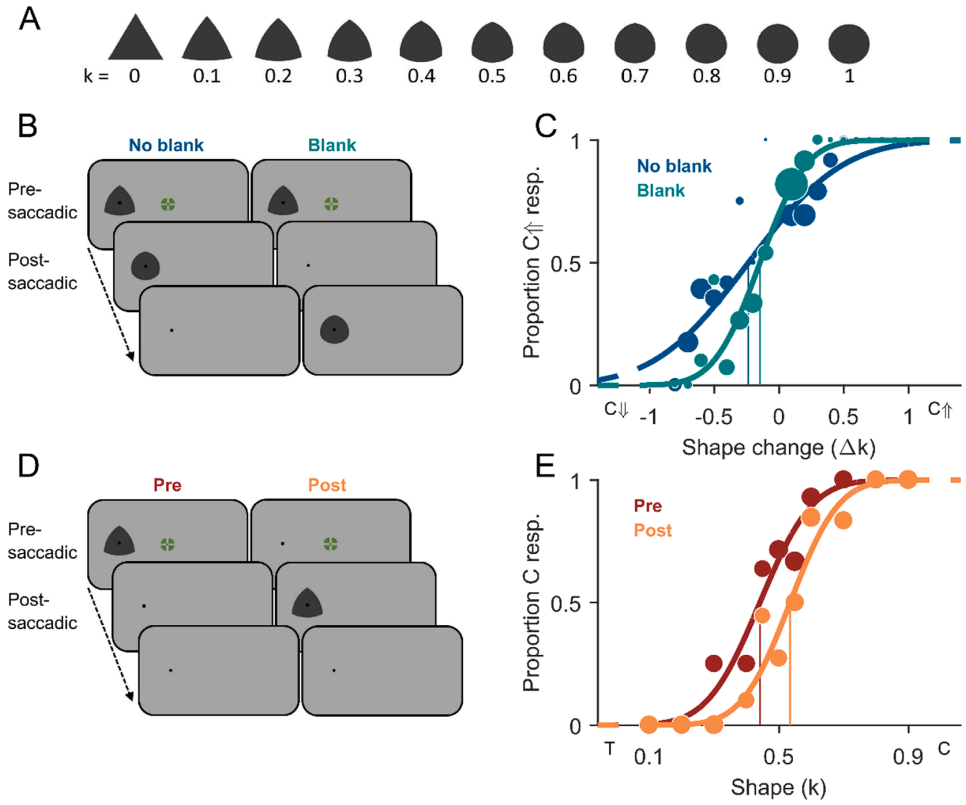


Fig. 1. Stimuli and methods of Experiment 1. A) All shape stimuli with curvature index k going from 0 (triangular, T) to 1 (circular, C). Circumradii were adjusted to keep the covered area approximately constant across shapes. **B)** Schematic trial procedure of Experiment 1A showing a shape change of circularity increase across a saccade, either with a blank screen after the postsaccadic stimulus (no-blank condition) or before (blank condition). **C)** Example psychometric functions of one representative participant fitted to proportion circularity-increase (C↑) responses over shape changes tested (Δk) with negative deltas indicating circularity decrease (C↓) and positive deltas indicating circularity increase (C↑). Dark-blue data points (size scales with number of valid measurements) and fit represent the no-blank condition, and green represents the blank condition. Vertical lines indicate the points of subjective stability. **D)** Schematic trial procedure of Experiment 1B, in which participants had to compare the observed shape to the overall mean shape. Shape stimuli were either exclusively presented before the saccade in the peripheral visual field (presaccadic condition) or exclusively after the saccade in the central visual field (postsaccadic condition). **E)** Example psychometric functions of one representative participant fitted to proportion more-circular (C) responses over shapes tested (k) for the pre- (dark red) and postsaccadic condition (orange). Vertical lines indicate the points of subjective equality. A shape with k = 0.5 represents the true mean shape over all shapes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

For example, if the change in a trial was assigned to −0.2 Δk, possible presaccadic shapes were all shapes except 0 and 0.1 k. If the change direction reported by the participant differed from the physical change direction the response was classified as a miss and the change magnitude was increased by a step size of 0.1 |Δk| for the next trial. If the reported change direction equalled the physical change direction, the response was classified as a hit and after two consecutive hits the change magnitude was decreased by the step size. Each staircase was running for 50 trials resulting in 400 trials in total for Experiment 1A. All conditions were tested interleaved and trial order was randomised. The design of Experiment 2A was similar to the one of Experiment 1A but the trial number for each staircase was 70 and there was no blanking condition, resulting in 280 trials for Experiment 2A. In Experiment 1B and 2B, 11 curvature values k (0.1, 0.2, 0.3, 0.4, 0.45, 0.5, 0.55, 0.6, 0.7, 0.8, 0.9) were tested for the presaccadic and postsaccadic condition with 15 repetitions each resulting in 330 trials. The two conditions were tested interleaved and trial order was randomised. In Experiments 1B and 2B participants completed a training of similar design as the main part of the experiment but without repetitions resulting in 22 trials. Training trials were excluded from analysis.

2.4. Equipment

For Experiment 1, stimuli were displayed on a VIEWPixx monitor at a 1920 × 1080 px resolution and a 120 Hz refresh rate. The display had a size of 51.5 × 29 cm and was viewed at a distance of 60 cm. The screen was calibrated to ensure a linear gamma correction and it had a luminance of 0.39, 54, and 105 cd/m^2 for black, grey, and white pixels respectively. Eye movements were recorded with a desktop-mounted EyeLink 1000 (SR Research Ltd., Ontario, Canada) with a sampling rate of 1000 Hz. For Experiment 2, stimuli were presented using a back-projection setup, using a PROPixx projector (VPixx Technologies, Saint Bruno, QC, Canada), with a resolution of 1920 × 1080 px and a refresh rate of 120 Hz, projected onto a 91 × 51-cm screen from Stewart Filmscreen (Torrance, CA). Viewing distance was 106 cm. The screen was calibrated to ensure a linear gamma correction and to minimize the central hot spot, and it had a luminance of 2.07, 71, and 140 cd/m^2 for black, grey, and white pixels respectively. Eye movements were recorded using a tower-mounted EyeLink 1000 Plus (SR Research Ltd., Ontario, Canada), with a sampling rate of 1000 Hz. Experimental software and analysis were written in MATLAB (Mathworks, Natick, MA, USA), using Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) for stimulus display and the EyeLink Toolbox (Cornelissen et al., 2002) for

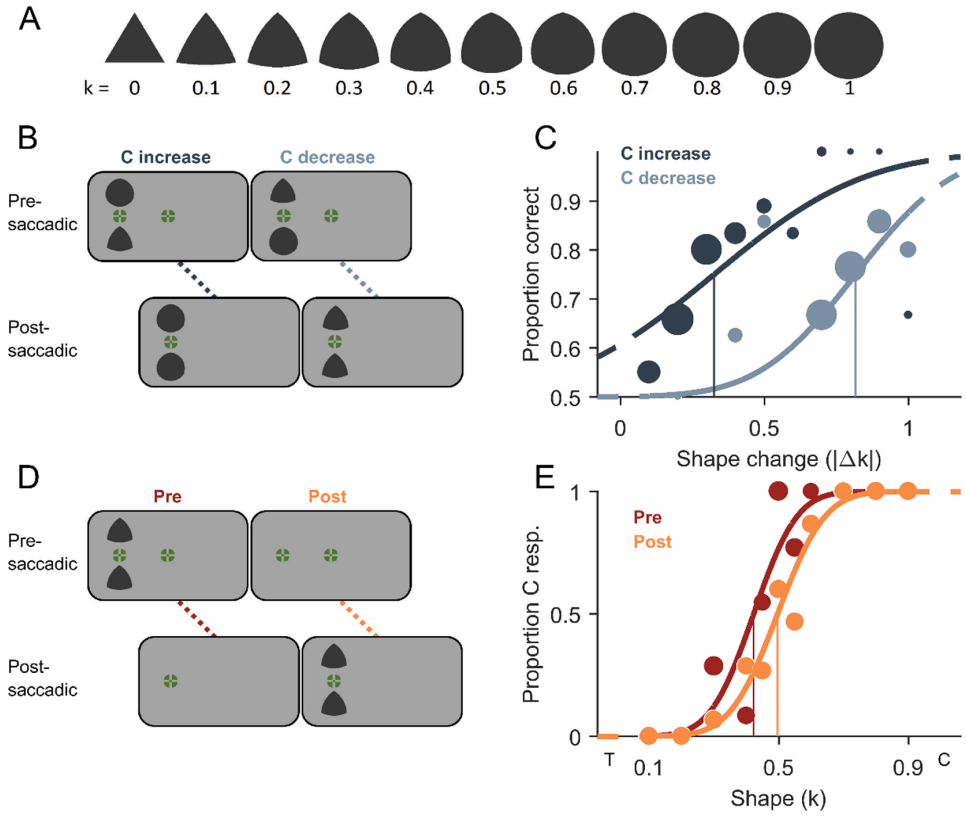


Fig. 2. Stimuli and methods of Experiment 2. A) All shape stimuli with curvature index k going from 0 (triangular, T) to 1 (circular, C). Circumradii were kept constant across all shapes. **B)** Schematic trial procedure of Experiment 2A showing a shape change of circularity increase across a saccade in the left column and a change of circularity decrease in the right column. Two shapes were presented simultaneously and only one changed its shape resulting in two identical shapes after the saccade. The position of the shape change had to be indicated. **C)** Example psychometric functions of one representative participant fitted to proportion correct responses over absolute shape change magnitudes (|Δk|) for the change direction of circularity increase (dark grey) and circularity decrease (light grey). Data point size scales with the number of valid measurements and the vertical lines indicate detection thresholds (75% correct). **D)** Schematic trial procedure of Experiment 2B, in which participants had to discriminate the observed shape from the overall mean shape. The two identical shape stimuli were either exclusively presented before the saccade in the peripheral visual field (presaccadic condition) or exclusively after the saccade close to the central visual field (postsaccadic condition). **E)** Example psychometric functions of one representative participant for the pre- (dark orange) and postsaccadic condition (light orange). Conventions are identical to Fig. 1E. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

eye tracker operation. Participants responded using a standard keyboard (vertical plus-sign button on number pad for towards-triangular or more-triangular responses and horizontal zero button on number pad for towards circular or more-circular responses; up- and down arrow keys for upper/lower responses in Experiment 2A) and their head position was stabilised using a forehead- and chinrest.

2.5. Procedure

Participants started each trial by pressing the space bar while fixating a central fixation stimulus. In Experiment 1A, the presaccadic shape appeared to the left or right at an eccentricity of 15° of visual angle on the horizontal axis after a duration jittered between 750 and 1500 ms. The participants were instructed to execute a saccade toward the centre of the peripheral shape, which was marked by a black dot (Fig. 1B). The fixation stimulus at screen centre remained on screen for additional 200 ms or until a saccade was detected. A trial was aborted when no saccade was detected within 1.8 s after saccade target onset. Upon saccade detection, the shape stimulus was replaced either immediately (no-blank condition), or removed (the black dot remained) for 200 ms (blank condition) and then replaced by the postsaccadic shape stimulus. The postsaccadic stimulus was displayed for half of the duration of the presaccadic stimulus in a given trial of the blank condition, and plus 30 ms in a given trial of the no-blank condition (to compensate for the time during the saccade). The extra time between trial start and response screen onset in a blank trial (due to the postsaccadic blank) was added to the no-blank condition but after the postsaccadic stimulus presentation; i.e., the central dot at saccade target position remained on screen for 170 ms. Finally, the blank screen prompted participants to give a response by button press, indicating whether the change was perceived as going toward a more triangular shape or toward a more circular shape. A high tone was played when the gaze behaviour in that trial was incorrect according to the criteria stated for trial exclusions below. A low tone was played when the response for the change direction was incorrect. No tone was played and the trial ended immediately after the response was given when gaze behaviour and response were correct.

In the trial procedure of Experiment 1B (Fig. 1D), either a shape stimulus plus central dot (presaccadic condition), or solely the black dot (postsaccadic condition) appeared presaccadically at an eccentricity of 15° of visual angle on the horizontal axis after a duration jittered between 750 and 1500 ms from trial start. Upon saccade detection, the presaccadic stimulus was either reduced to the uninformative central dot (presaccadic condition: shape information only presaccadically) or

the shape stimulus was added (postsaccadic condition: shape information only postsaccadically). Postsaccadic-stimulus presentation duration equalled half the participant's median presaccadic-stimulus presentation duration over all completed trials of the presaccadic condition plus 30 ms. After the postsaccadic shape stimulus offset, the black target dot remained on screen for another 170 ms. The consecutive blank screen prompted participants to give a response by button press indicating, whether the perceived shape was more triangular or more circular than the mean of all shapes seen thus far. There was no feedback given on the correctness of the response but a high tone was played for irregular gaze behaviour similarly to part A. In the 22 training trials, both kinds of feedback were given. The order of completion of part A and B was counterbalanced across participants and data was collapsed across order (AB or BA) as analysis revealed no effect of order.

The procedures of Experiment 2A (Fig. 2B) and B (Fig. 2D) were similar to the one of Experiment 1A and B respectively, except that two shape stimuli (without central black dots) were shown pre- and postsaccadically, one below and one above a second fixation stimulus centred between them, with a distance of 2.5° between the centre of one shape and the centre of the second fixation stimulus. Eccentricity from the first fixation stimulus was ± 5° on the horizontal axis. In Experiment 2A, the two shapes were always different presaccadically and identical postsaccadically and responses were given to indicate the location of the shape change (top or bottom). The presentation duration of the postsaccadic stimuli equalled half the presentation duration of the presaccadic stimuli on a given trial. In Experiment 2B, the presentation duration of the postsaccadic stimuli equalled half the participant's median presentation duration of the presaccadic stimuli over all completed trials of the presaccadic condition and the empty response screen followed the postsaccadic shape stimuli offset immediately.

2.6. Eye-movement analysis and trial exclusions

For eye-movement data analysis saccades were detected offline using the EyeLink 1000 algorithm (velocity threshold = 22°/s, acceleration threshold = 3800°/s^2). Saccade onset was defined as the first sample after saccade-target onset in which a saccade was detected; likewise, saccade offset was defined as the last sample after saccade onset in which a saccade was detected. Postsaccadic landing position was taken at the point of saccade offset. Saccade latency was defined as the time (resolution of 1 ms) between saccade-target onset and saccade onset. Results regarding saccade latencies can be found in the Supplementary material.

Trials, which contained blinks in the time between 300 ms to saccade-target onset and response-screen onset, trials, in which the switch between pre- and postsaccadic stimulus was not achieved in the time of the saccade (e.g., due to small, consecutive saccades instead of one large saccade), and trials, in which not the full sequence of events was run through were excluded from analysis. We further excluded trials with saccade latencies below 50 ms or above 600 ms. Further trials were excluded when gaze position deviated more than 2° on the horizontal axis or more than 1.5° on the vertical axis, from saccade target centre in the time between saccade landing and shape stimulus offset. In total, 11 ± 10% (mean ± standard deviation, over participants and conditions) of trials were excluded from Experiment 1A, 17 ± 10% from Experiment 1B, 5 ± 4% from Experiment 2A, and 10 ± 9% from Experiment 2B.

2.7. Psychophysical analysis

To obtain psychometric functions for each participant for Experiments 1A (Fig. 1C), perceptual choices were converted into proportion circularity-increase responses for each shape change tested. A cumulative Gaussian was fitted to the data using psignifit 4.0 toolbox (Schütt et al., 2016). The point of subjective stability (PSS) was estimated as the magnitude and direction of shape change (Δk) corresponding to 50% circularity-increase responses. A negative PSS indicates a bias for reporting circularity-increase shape changes. The just-noticeable difference (JND) was defined as the standard deviation of the cumulative Gaussian, with a lower JND indicating higher precision for shape-change discrimination.

Similarly to the data analysis for Experiment 1A, responses in Experiment 1B and 2B were converted into proportion more-circular (than the mean shape) responses for each shape tested, and psychometric functions were fitted (Fig. 1E, Fig. 2E). The point of subjective equality (PSE, parameter equivalent to PSS) was estimated as the degree of curvature (k) corresponding to 50% more-circular responses. A PSE above 0.5 indicates a bias for perceiving shapes as more triangular; accordingly, a PSE below 0.5 indicates a bias to perceive shapes as more circular. The just-noticeable difference (JND) was defined as the standard deviation of the cumulative Gaussian, with a lower JND indicating higher precision for shape discrimination.

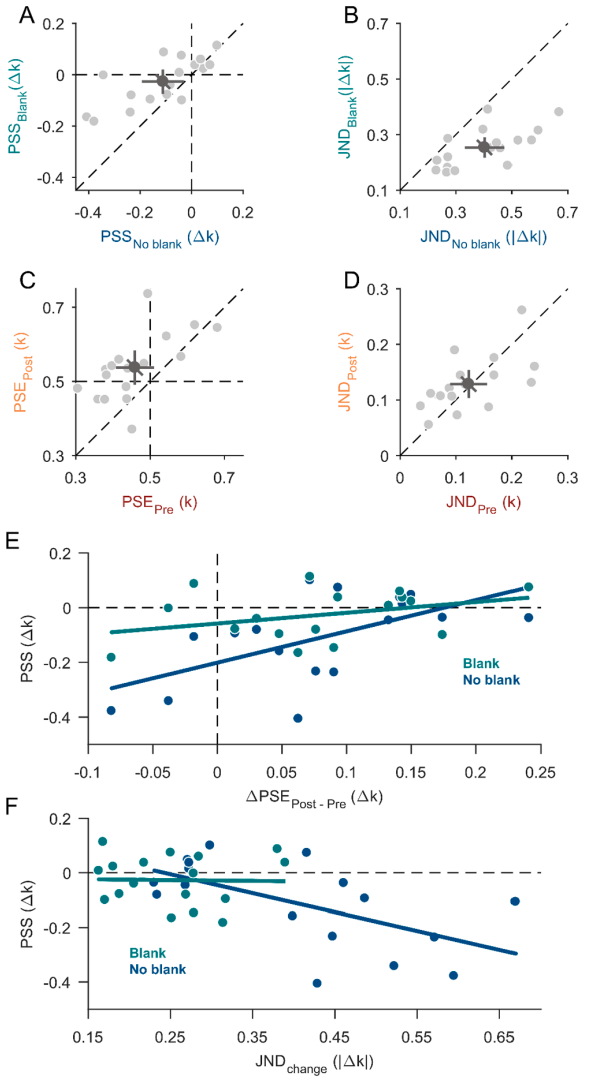
Perceptual choices in Experiment 2A were converted into proportion correct responses for each shape change magnitude tested for both change-direction conditions. A cumulative Gaussian starting at chance level of 50%-correct responses was fitted to the data for each participant using psignifit 4.0 toolbox (Schütt et al., 2016). The detection threshold was estimated as the absolute magnitude of shape change (|Δk|) necessary for a participant to reach 75%-correct responses. A lower threshold indicates higher sensitivity to the corresponding shape-change direction (Fig. 2C). For all statistical tests, the alpha value was set to 0.05 and t-tests were two-tailed.

3. Results

3.1. Experiment 1 – Shape perception biases and blanking effect

In Experiment 1A, we increased or decreased the circularity of the shape stimulus during the saccade and asked participants to report the perceived direction of the change. The mean point of subjective stability (PSS) was −0.11 ± 0.16 Δk for the no-blank condition and −0.03 ± 0.09 Δk for the blank condition (Fig. 3A). The mean PSS for the no-blank condition was significantly different from zero ($t(16) = -2.89$, $p = 0.011$) indicating that participants had a bias to report transsaccadic shape changes of increasing circularity. A tendency for such a bias was also observed in the blank condition but it was not significantly different from zero ($t(16) = -1.21$, $p = 0.243$) and the difference between PSS for the no-blank and blank condition was significant ($t(16) = -3.20$, $p = 0.006$). The mean just-noticeable difference (JND) for shape change discrimination in Experiment 1A was 0.40 ± 0.14 |Δk| for the no-blank condition and 0.25 ± 0.07 |Δk| for the blank condition (Fig. 3B). JNDs were significantly different ($t(16) = 5.85$, $p < 0.0001$) between blanking conditions. In sum, participants were significantly more precise (JNDs) and more accurate (PSS) at discriminating shape-change direction in the blank condition compared to the no-blank condition. This result indicates a blanking effect for shape changes.

In Experiment 1B, we measured the appearance of the shapes presaccadically in the periphery and postsaccadically in the fovea. The mean point of subjective equality (PSE) in Experiment 1B was 0.46 ± 0.10 k for the presaccadic condition and 0.54 ± 0.09 k for the postsaccadic condition (Fig. 3C). The mean PSE for the presaccadic condition ($t(16) = -1.70$, $p = 0.109$) and postsaccadic condition ($t(16) = 1.72$, $p = 0.107$) were both not significantly different from the true mean of the shape stimuli of 0.5 k, but significantly different from each other ($t(16) = -3.93$, $p = 0.0012$). This indicates that participants perceived the shapes on average as more circular presaccadically in the periphery and as more triangular postsaccadically in the fovea. The mean just-



(caption on next column)

Fig. 3. Results from Experiment 1. A) Scatter plot for all points of subjective stability (PSS) compared between the no-blank condition (horizontal axis) and blank condition (vertical axis) of Experiment 1A. Data points left from the dashed vertical line or below the dashed horizontal line (negative PSS) indicate a bias for circularity-increase changes. **B)** Scatter plot for just-noticeable differences (JNDs) compared between the no-blank condition (horizontal axis) and blank condition (vertical axis) of Experiment 1A. Data points below the diagonal dashed line indicate that participants were more precise in the blank condition. **C)** Points of subjective equality (PSE) compared between pre- and postsaccadic condition in Experiment 1B. Data points above the dashed diagonal line indicate a less circular appearance in the postsaccadic condition compared to the presaccadic condition. **D)** Just-noticeable differences (JNDs) compared between pre- and postsaccadic condition in Experiment 1B. **A-D)** Data points on the dashed diagonal line indicate no difference between conditions. Light-grey dots represent individual participant data and the dark-grey dot indicates the overall mean. The error bars indicate 95%-confidence intervals within each condition (cardinal bars) or between conditions (oblique bar). **E)** The effect of individual perceptual differences between pre- and postsaccadic vision (difference of PSEs from Experiment 1B, horizontal axis) on the bias in the change-discrimination task (PSS from Experiment 1A, vertical axis) separately for the blank (green) and no-blank condition (dark blue). The more positive a PSE difference, the stronger a bias for perceiving shapes as more circular presaccadically and the more negative a PSS, the stronger was the bias for circularity-increase changes. Linear regression fits for each blanking condition are represented by the coloured solid lines. **F)** The effect of individual precision (JNDs, horizontal axis) on the bias (PSS, vertical axis) in the change-discrimination task of Experiment 1A separately for the blank (green) and no-blank condition (dark blue). Increasing JNDs indicate decreasing precision and the more negative a PSS the more of a circularity-increase bias was observed. Linear regression fits for each blanking condition are represented by the coloured solid lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

noticeable difference (JND) in Experiment 1B was 0.13 ± 0.05 k for the presaccadic condition and 0.12 ± 0.06 k for the postsaccadic condition (Fig. 3D). The difference in JNDs between the pre- and postsaccadic condition was not significant ($t(16) = 0.43$, $p = 0.675$), which indicates that participants were equally precise at discriminating shapes from the mean shape pre- and postsaccadically[1].

Most interestingly, the overall bias in the change discrimination task (PSS in Experiment 1A) cannot be explained by a direct influence of appearance differences between presaccadic peripheral and postsaccadic foveal vision (differences between PSEs in Experiment 1B). In fact, the more circular appearance in pre- compared to postsaccadic vison should increase the perceived change magnitude for circularity-decrease but participants showed a bias to report circularity-increase changes instead (see also Figure S1). To obtain a more detailed insight into the relationship between appearance differences and change discrimination biases, we analysed the impact of individual differences between pre- and postsaccadic shape perception (differences between pre- and postsaccadic PSEs of Experiment 1B) on participants' biases (PSS of Experiment 1A) in the change discrimination task (Fig. 3E). A positive correlation between the PSE differences and PSS was observed for the no-blank condition (slope $m = 1.14$, $p_m = 0.017$, y-intercept $n = -0.20$, $p_n < 0.001$, $r^2 = 0.33$) and a similarly oriented but non-significant relationship for the blank condition ($m = 0.44$, $p_m = 0.172$, $n = -0.06$, $p_n = 0.09$, $r^2 = 0.12$). The positive slope may suggest that perceptual differences between pre- and postsaccadic perception do have a direct influence on transsaccadic change perception. Participants who perceived the shapes on average as more triangular postsaccadically than presaccadically (positive PSE differences in Fig. 3E) showed a smaller bias to disproportionally often report changes with circularity increase (PSS

[1] Note that this result would not be expected given the typical superiority of central compared to peripheral vison; but it was intended by our design as we halved the postsaccadic presentation duration in relation to the presaccadic presentation duration.

values closer to zero in Fig. 3E). Above and beyond this direct influence, the significantly negative intercept for the no-blank condition again shows that there was a bias to report circularity increase more often. The origin of this bias remains an open question that we will address in the discussion.

As we observed that the overall circularity-increase bias was reduced in the blank condition, where participants also were more precise (lower JNDs in part A) we further tested whether the magnitude of the bias was related to the precision across participants. The negative correlation for the no-blank condition ($m = -0.70$, $p_m = 0.015$, $n = 0.17$, $p_n = 0.131$, $r^2 = 0.33$) shown in Fig. 3F indicates that lower precision in change discrimination was accompanied by a larger bias. The smaller variance across JNDs in the blank condition did not seem to affect the bias ($m = -0.01$, $p_m = 0.981$, $n = -0.02$, $p_n = 0.811$, $r^2 < 0.01$). These results indicate that participants who had a harder time discriminating intra-saccadic shape changes (showed greater JNDs) benefited most from the circularity-increase change direction in terms of detectability (more negative PSS). Similarly, when there was a postsaccadic blank (i.e., JNDs were low) both change directions were equally well detectable.

3.2. Experiment 2 – Perceptual bias for circularity-increase changes

In Experiment 1A, we observed a bias for circularity-increase reports that led to a shift of the PSS. Theoretically, this bias alone could be interpreted as a perceptual bias, a response bias for one response alternative or even a response bias for one of the two response keys. However, the correlation between the bias in Experiment 1A and the differences in pre- and postsaccadic appearance in Experiment 1B (Fig. 3E) cannot be explained by any response bias and strongly suggest a perceptual bias. To provide further evidence that this was a perceptual bias and not a mere response bias for one response alternative or for one response key, we performed Experiment 2. Here, a pair of shape stimuli was shown before and after the saccade and only one stimulus changed its shape during the saccade. Participants had to report which of the two stimuli was changed. The mean detection threshold was 0.53 ± 0.20 $|\Delta k|$ for the circularity-decrease condition and 0.33 ± 0.10 $|\Delta k|$ for the circularity-increase condition (Fig. 4A). Detection thresholds were significantly lower when shapes increased in circularity across a saccade compared to a circularity decrease ($t(12) = 3.97$, $p = 0.002$). This result replicates the change-direction bias observed in Experiment 1A and rules out the possibility of a response bias, meaning that participants not only reported but also perceived circularity-increase changes disproportionally often. In other words, the most likely explanation for the circularity-increase bias in PSSs in Experiment 1 are the lower detection thresholds for circularity increases compared to circularity decreases in Experiment 2.

Similarly to Experiment 1B, we measured the appearance of the shapes presaccadically in the periphery and postsaccadically near the fovea in Experiment 2B. The mean point of subjective equality (PSE) from Experiment 2B was 0.42 ± 0.06 k for the presaccadic condition and 0.46 ± 0.06 k for the postsaccadic condition (Fig. 4B). The mean PSE of the presaccadic condition was significantly different from the true mean of 0.5 k ($t(12) = -4.68$, $p < 0.001$), but that of the postsaccadic condition was not ($t(12) = -2.14$, $p = 0.053$). Mean PSEs of both conditions were significantly different from each other ($t(12) = -5.57$, $p < 0.001$). This replicates the finding from Experiment 1B that participants perceived the shapes on average as more circular presaccadically in the peripheral visual field and as more triangular postsaccadically near the central visual field. The mean just-noticeable difference (JND) from Experiment 2B was 0.12 ± 0.05 k for the presaccadic condition and 0.13 ± 0.05 k for the postsaccadic condition (Fig. 4C). The difference in JNDs between the pre- and postsaccadic condition was not significant ($t(12) = -1.11$, $p = 0.291$), which indicates that participants were equally precise at discriminating shapes from the mean shape pre- and postsaccadically, as it was the case in Experiment 1B.

4. Discussion

In this study, we investigated the perception of shape changes during saccadic eye movements and its relationship to pre- and postsaccadic appearance of shape. Our results confirm that transsaccadic perception of shape changes underlies the same effects that apply to similar (Deubel et al., 2002, Experiment 3; Grzeczkowski, van Leeuwen, et al., 2020) and other object features: performance at intrasaccadic change detection was relatively poor under normal conditions (no-blank condition) and an accompanying postsaccadic blank facilitated change detection (Fig. 3B). On the other hand, shape changes seem to be extraordinary (but see section 4.3 Transsaccadic expectations and other feature changes) as the direction of change influenced change detectability under normal conditions such that changes with increased circularity were detected more often than changes with decreased circularity (Fig. 3A & Fig. 4A). We could rule out that this was due to a simple response bias for choice category as we implemented a criterion-free paradigm in Experiment 2. We can also rule out the possibility that the bias in shape-change discrimination might be due to changes in size (circumradius) or covered area between shapes as we fixed one of these metrics in each experiment (Fig. 1A & Fig. 2A).

We found that shape appearance was distinct between pre- and postsaccadic perception such that shapes generally appeared more circular presaccadically in the peripheral visual field (at 15° in Experiment 1, and at 5° in Experiment 2) compared to postsaccadically in the fovea (Experiment 1, Fig. 3C) or near it (Experiment 2, Fig. 4B). This means that the differences in appearance cannot directly explain the overall bias in the perception of shape-changes in terms of a perceptual increase

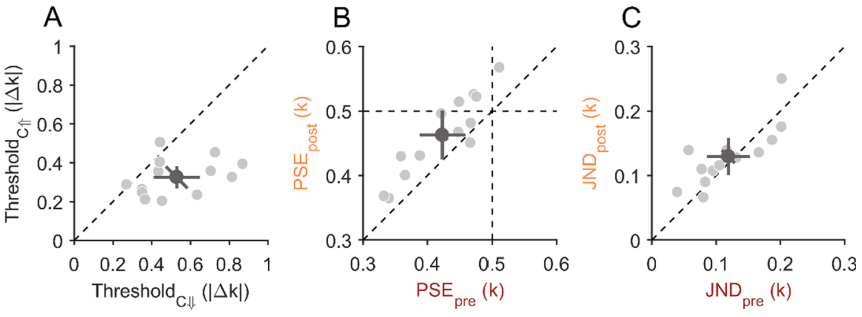


Fig. 4. Results from Experiment 2. A) Scatter plots for all detection thresholds compared between the circularity-decrease (C↓, horizontal axis) and circularity-increase condition (C↑, vertical axis) of Experiment 2A. Data points below the diagonal dashed line indicate lower thresholds for the circularity-increase change direction. **B)** Points of subjective equality (PSE) compared between pre- and postsaccadic condition in Experiment 2B. PSEs below 0.5 indicate a participant's bias for disproportionally often judging shapes to be more circular. Data points above the dashed diagonal line indicate a less circular appearance in the postsaccadic condition compared to the presaccadic condition. **C)** Just-noticeable differences (JNDs) compared between pre- and postsaccadic conditions in Experiment 1B. Data on the diagonal dashed line indicate that participants were equally precise in both conditions. **A-C)** Light-grey dots represent individual participant data and the dark-grey dot indicates the overall mean. The error bars indicate 95%-confidence intervals within each condition (cardinal bars) or between conditions (oblique bar).

of the circularity-increase change magnitude. In fact, a more circular appearance of shape in the periphery should reduce the magnitude of a shape change that increased circularity across a saccade. Our finding on appearance differences may be compared to other findings on appearance differences between peripheral and foveal vision. For example, it was shown that stimulus size appears smaller in the periphery (Newsome, 1972), and numerosity (number of dots in a dot cloud) appears lower in the periphery (Valsecchi et al., 2013; but see Hübner & Schütz, 2017). What determines less triangular appearance in the periphery might be related to what causes the size or numerosity reduction (see also section 4.2 Shape across the visual field). However, we want to emphasise that our and these other findings on visual-field differences in the appearance of visual features are not directly comparable. Pre- and postsaccadic perception are not equivalent to mere perception at the periphery and fovea. This may especially be the case for spatial features such as spatial frequency, numerosity, or shape since it has been shown that the preparation of a saccade abolishes visual crowding (Harrison et al., 2013), and enhances spatial resolution (Li et al., 2016; 2019). Measuring pre- and postsaccadic appearance represents a more complete account in regard to transsaccadic perception. This may be especially evident considering that presaccadic appearance likely results from an integration of presaccadic sensory information with the prediction for the postsaccadic outcome (e.g., Herwig et al., 2015; Valsecchi & Gegenfurtner, 2016). This integration will inevitably make pre- and postsaccadic appearance more similar.

We further found that inter-individual variations of pre- and postsaccadic differences (differences between PSEs of Experiment 1B) systematically influenced shape-change perception (shifts in the PSS of Experiment 1A) as shown by a significant positive correlation between the two (Fig. 3E). This correlation can only be based on a perceptual bias and cannot be explained by any response bias. Taken together, our results may suggest that visual-field differences have a direct and an indirect influence on transsaccadic perception of shape changes. The direct influence is based on the distinct appearance of shape pre- and postsaccadically; if a shape appears more circular before than after the saccade, shape changes with circularity increase should have a smaller perceptual magnitude and be missed more easily than changes with circularity decrease. However, the perceived magnitude of a shape change only seems to play a subsidiary role as we found an overall bias in the opposite direction. Change direction predominantly affected shape-change perception and this may be due to visual field differences as well, but indirectly. We suggest that a life-time experience of appearance changes leads to the build-up of transsaccadic expectations[2] that serve as a measure for the visual system to evaluate perceptual evidence for or against external stability. One might infer from the pre- and postsaccadic appearance differences of shape that the typical experience of the visual system should be a circularity decrease in saccade direction (perceived circularity is higher presaccadically than postsaccadically) and that similar experiences with real-world shapes have formed the expectation responsible for the observed bias. The principal assumption we make is that a contradiction of such an expectation, i.e., a circularity-increase change should be evaluated as strong evidence against stability and facilitating change detection, leading to the overall bias for circularity increase. It seems likely that participants, who relied more strongly on expectations than others benefited more from a circularity-increase change i.e., showed a stronger circularity-increase bias and also showed smaller differences in pre- and postsaccadic appearance (as presaccadic appearance would more strongly be influenced by the prediction).

According to formulations in predictive coding theory (Feldman & Friston, 2010; Bastos et al., 2012), participants who rely more on predictions and down-weight predictions errors should also show lower sensory precision. Evidence following this line comes from the correlation of individual differences in change-discrimination precision (JNDs in Experiment 1A) with individual bias strength (Fig. 3F). Participants who were less precise might have down-weighted predictions errors (in classical terms: they had a stronger assumption of stability) and hence, tolerated larger discrepancies between pre- and postsaccadic information. Those participants revealed a larger circularity-increase bias, which suggests that this change direction caused prediction errors strong enough to make the external change detectable despite the down-weighting. It should, however, be mentioned that increased change-discrimination precision might also be due to larger pre- and postsaccadic appearance differences in those participants, which, potentially, facilitated the detection of circularity-decrease changes more than it impaired the detection of circularity-increase changes (Figure S2). Given trials with a postsaccadic blank, JNDs were overall smaller, a circularity-increase bias was nullified, and there was no more correlation between individual precision and bias strength. This pattern of results would be expected if a postsaccadic blank already caused a maximally large prediction error (in classical terms: abolished the stability assumption) and there would have been nothing left for strong evidence coming from a circularity-increase change to add.

4.1. Transsaccadic expectations

A striking commonality amongst all visual events that improve intrasaccadic change detection performance is that they are unexpected with respect to what can be learned from every-day transsaccadic experience (O'Regan & Noë, 2001). For example, discrepancies between saccade landing position and postsaccadic target position (referred to as retinal error) in parallel to saccade direction are "experienced" by the visual system to a greater degree due to an individual's natural landing variability (van Opstal & van Gisbergen, 1989; Niemeier et al., 2003). On the contrary, orthogonal displacements place saccade targets outside the typically experienced, oval window of saccade landing variability (Niemeier et al., 2007; Wexler & Collins, 2014; Atsma et al., 2016). Such an orthogonal error should contradict what could be learned from every-day experiences and therefore facilitate detection of a change. A second example may be that visual disruption that can be anticipated by the visual system, such as the visual blank caused by blinks, does not facilitate transsaccadic change detection in contrast to externally imposed blank periods (Deubel et al., 2004). In general, it seems that less frequently experienced discrepancies reach consciousness and facilitate change detection while more frequently experienced discrepancies fail to reach consciousness and change detection is suppressed. Similarly, we show that, due to pre- and postsaccadic appearance differences, the typical transsaccadic experience of shape is that circularity decreases in saccade direction. Appearance differences experienced throughout life might form transsaccadic expectations about the typical magnitude and, importantly, the typical direction of change. Hence, changes that are opposite to the expected change direction should lead to an increased error or may be taken as strong evidence for a change in the external world, reducing the impact of an assumption of external stability[3].

[2] We use the term *expectation* to refer to implicit knowledge about the typical transsaccadic percept (the change from pre- to postsaccadic appearance resulting from a shift of feature information across the visual field). This knowledge should be acquired form life-time experience of such transsaccadic contingencies. The term *prediction* will be used to refer to the visual signal that is generated on demand by higher-level areas and that is based on presaccadic information and on transsaccadic expectations.

[3] We use the term stability assumption not as a reference for a general tendency to assume stability but as one of two possible outcomes of the evaluation of transsaccadic information. The stability assumption may be a generalised phrase to refer to learned contingencies observed in our typically stable world, i.e., it represents the knowledge of re-occurring patterns of (visual) information resulting from eye- or body motion, and observations that are in accordance with this experience do not reach consciousness (the world remains stable).

Change detection facilitation due to a specific change direction has, until now, only been reported for saccade target displacements (McConkie & Currie, 1996; Niemeier et al., 2007; Wexler & Collins, 2014; Atsma et al., 2016; Souto et al., 2016). The underlying concepts of two models (Niemeier et al., 2003; Atsma et al., 2016) that can explain such a facilitation for target displacements orthogonal- compared to parallel to saccade direction may be similar to what was first suggested by MacKay (1972); namely, a dichotomy between the two possible scenarios of either an external change or no external change for or against which evidence can be evaluated based on transsaccadic expectations. Transsaccadic predictions appear to be the measure for the visual system by that transsaccadic expectations (experience-based knowledge on transsaccadic contingencies) become effective. To give a simplified example, if the visual system has learned that shapes typically become more triangular across a saccade, the visual signal that gets generated for, e.g., a medium shape of $k = 0.5$ in the periphery, should be of a more triangular shape (e.g., $k = 0.1$) and fed back to lower visual areas before the postsaccadic information arrives. The discrepancy (also referred to as prediction error in predictive coding) between this prediction (that relies on presaccadic sensory information and transsaccadic expectations) and the actual postsaccadic shape should be larger when the postsaccadic shape is more circular (e.g., $k = 0.7$), than when the postsaccadic shape information would be more triangular (e.g., $k = 0.2$), and a larger error should facilitate change perception. The overall bias we found for circularity increase suggests that a transsaccadic prediction (more triangular), rather than the presaccadic information (more circular), is compared to the postsaccadic information. An integration of the prediction with the presaccadic input may take place subsequently and, possibly, only when no postsaccadic input was available e.g., when presaccadic appearance is tested. Models on intrasaccadic change perception (e.g. Atsma et al., 2016) should incorporate transsaccadic predictions that are specific to the learned transsaccadic contingencies of the feature at hand.

Alternative theoretical accounts for intrasaccadic change detection have been proposed to explain benefits from target blanking and are based on the potential benefit provided by the extra amount of input-free time during the blank period, enabling either a sufficient read-out of the presaccadic target information, or providing sufficient time to process upcoming postsaccadic information outside the time window of suppression of contrast sensitivity (e.g. Zimmermann et al., 2013; Ziesche et al., 2017). Such accounts fail to offer a potential explanation for our shape-change direction bias, and a row of other findings on transsaccadic change perception. For example, the improvement of displacement detection due to accompanying object-form changes (Demeyer et al., 2010) or other accompanying feature changes (Tas et al., 2012), or a stronger blanking effect for children compared to adults (Stewart, Hübner, & Schütz, 2020). Overall, an account based on evidence evaluation for or against a stable transsaccadic percept appears to be the more comprehensive theory for visual stability across saccades and, with consideration of feature-specific transsaccadic expectations, the most likely theory behind our findings.

4.2. Shape across the visual field

Assuming that transsaccadic expectations led to the observed circularity-increase bias, it should be evaluated what the particular character of the typically experienced saccade-induced contingency is, that could have led to such an expectation. To do that, we need to evaluate what determines shape information in the periphery compared to the fovea. We know that the peak of the spatial contrast sensitivity function is shifted to lower spatial frequencies in the periphery compared to the fovea (e.g., Rovamo et al., 1992), which may imply that two intersecting lines or edges become less visible in the periphery the smaller the angle separating them (the sharper a corner). In addition, spatial localisation of available visual information is more difficult in the periphery (Rentschler & Treutwein, 1985; Levi & Klein, 1986; Hess & Hayes, 1994), potentially leading to distorted shape information and edges that are spatially misaligned. Illustrations of the approximated distortion in low-level peripheral processing for shape can be found in the work by Valsecchi et al. (2018), who manipulated overlapping geometric shape stimuli using an image-manipulation algorithm that was designed to simulate all aspects of low-level peripheral processing (Eidolon factory, Koenderink et al., 2017). Taken together, these studies point at two key properties that might determine low-level shape information across the visual field: spatial detail (sharpness) and shape continuity (degree of distortion).

Our finding that shapes are perceived as more circular in the periphery (Fig. 3C & Fig. 4B) could be caused by the limited processing capacity of both of these properties. Fine corners were either not represented for the lack of visual detail or they were mis-localised to some degree that gave the impression of not being part of the figure/shape. Alternatively, they might be removed in order to rectify spatial disarray in the periphery. For instance, perceptual illusions such as the honeycomb illusion (Bertamini et al., 2016, 2019) may indicate that fine visual detail is reasonably well resolvable and localisable in the periphery but becomes less visible for the sake of a simple geometrical shape representation. Consistently with this interpretation, Valsecchi and colleagues (2018) showed that irregular shapes appear less irregular in the periphery than in the fovea; and it is known that feedback information is at the basis of shape perception (e.g., Hupé et al., 1998; Murray et al., 2002; Kok & de Lange, 2014). This would mean that for our intermediate shapes, even when corners could be resolved and located presaccadically they might have been rationalised to represent a circle as a less ambiguous shape.

In conclusion, all possibilities predict that spatial detail such as corners should rather add to an object's shape across a saccade than disappear. This may be due to the lower resolution, higher localisation uncertainty, or some mid-level rationalisation for circles in the periphery. Given that this low- or mid-level discrepancy was measurable between pre- and postsaccadic appearance (Fig. 3C & Fig. 4B) we cannot identify whether transsaccadic expectations were learned from appearance differences or from lower-level differences.

4.3. Transsaccadic expectations and other feature changes

Shape is known to mediate object constancy (Kayaert et al., 2003; El-Shamayleh & Pasupathy, 2016) and may even be one of the most relevant properties for the deduction of laws following from sensorimotor contingencies (e.g., Koenderink, 1985; O'Regan & Noë, 2001). Nevertheless, there might or should be transsaccadic expectations for other object feature changes. The nature of such an expectation might strongly depend on or be determined by the compensation mechanism that the visual system uses to work around the processing limitations of peripheral vision. In other words, the build-up of transsaccadic expectations may be based on appearance of stimuli rather than on the earlier visual information. Recent findings by Cicchini et al. (2021) support this assumption demonstrating that visual priors in serial dependence are based on illusory stimulus properties rather than on physical ones. The authors also showed that those priors interact, however, with the physical rather than the illusory properties of a current stimulus. This complex interplay of prior expectations and stimulus appearance versus the early sensory information induced by it make stimulus features interesting that reveal an oppositional relationship between early versus later stimulus information and in foveal versus peripheral vision.

For example, high spatial frequency gratings are harder to make out in the periphery (e.g., Rovamo et al., 1992), reflecting a reduced availability of early, high spatial frequency information. On the other hand, spatial frequency has been shown to appear higher in the periphery compared to the fovea (Davis et al., 1987). Models on explaining the appearance difference across the visual field have been favouring a spatial-frequency channel-labelling mechanism (Davis et al., 1987; Davis, 1990). While these relationships would have to be confirmed by

measuring pre- and postsaccadic appearance, a bias to perceive spatial frequency as higher in the periphery should lead to a transsaccadic expectation that predicts decreasing spatial frequency across saccades. It follows that changes that increase spatial frequency across saccades should be perceived more often. If this were true, it would also mean that transsaccadic expectations are built on appearance information rather than on low-level information. This hypothesis may be contradicted by Weiß et al. (2015), who did not report a bias in change detection for spatial frequency. However, since it was not the experimental goal of Weiß et al. (2015) to investigate a change-direction bias, the measurement applied in this study might not have been suited optimally for this purpose and further investigation may be needed here.

It may also well be, that the more complex a stimulus becomes i.e., the more feature dimensions the visual system can work with (e.g., colour + shape + luminance, or even feature combinations across modalities, see Stuckenberg et al., 2021), the more learned contingencies can be applied and compared to the incoming transsaccadic information. An accumulation of agreements with transsaccadic expectations for every feature may outweigh contradictions with transsaccadic expectations on spatial position such as large displacements or even blanks. This may become apparent in intrasaccadic displacement studies that found higher detection thresholds for naturalistic stimuli (McConkie & Currie, 1996); or a smaller blanking effect with complex stimuli (Tas et al., 2012; Stewart, Hübner, & Schütz, 2020).

Finally, the influence of transsaccadic expectations may be manifold and become apparent not solely in conscious categorisation but also in reaction time (Huber-Huber et al., 2019; Stewart, Hübner, & Schütz, 2020; Huber-Huber & Melcher, 2021) or, potentially, fixation duration (e.g. Henderson & Hollingworth, 2003), and pupil dilation (Preuschoff et al., 2011). Transsaccadic learning, that is the short-term learning of highly repetitive transsaccadic contingencies (e.g. Cox et al., 2005; Herwig & Schneider, 2014; Weiß et al., 2014; Valsecchi & Gegenfurtner, 2016), may also be affected by (long-term) transsaccadic expectations: on the one hand, larger prediction errors in one change direction might result in an increased updating of transsaccadic predictions and hence cause a larger learning effect (Rescorla & Wagner, 1972). One the other hand, larger prediction errors might be interpreted as evidence of object discrepancy as in causal-inference models (Körding et al., 2007; Atsma et al., 2016) and lead to a relatively weaker learning effect (Köller et al., 2020). Interestingly, in a transsaccadic-learning study that used the same shape stimuli as here, the participant group that experienced circularity increases across saccades showed an overall larger learning effect than the group that learned circularity decreases (Paeye et al., 2018, Experiment 2). However, it is unclear whether this difference between groups reflects a genuine difference in learning or whether it is due to differences in the baseline conditions between groups (judgements for unchanged objects). Furthermore, this difference was not always present (Paeye et al., 2018, Experiment 1). Further investigation would be needed to isolate an effect of long-term transsaccadic expectations on short-term learning of transsaccadic contingencies.

In summary, the character of transsaccadic expectations is likely to be specific for every visual feature dimension. Contradictions of and agreements with expectations in one feature dimension might affect change perception in general (for any other feature dimension) and may also be accumulated for or against external stability. In addition to change perception, transsaccadic expectations might affect several behavioural and perceptual measurements.

5. Conclusion

We found an overall shape-change direction bias for predominantly perceiving intrasaccadic shape changes that increased circularity across saccades. We further found that shape was perceived as more circular in presaccadic peripheral vision compared to postsaccadic foveal vision; but this appearance difference cannot directly explain the circularity-increase bias. We did, however, find a modulation of the overall bias on an inter-individual level presumably following from a direct but subsidiary influence of the appearance difference on the perceived magnitude of intrasaccadic shape changes. We conclude that the overall bias was due to an indirect influence of appearance differences across the visual field via a life-time learning of transsaccadic contingencies i.e., the built-up of transsaccadic expectations. This concept links transsaccadic perception of change or visual stability to a predictive-coding framework and implications following from this concept for other visual features in transsaccadic perception remain to be tested in the future.

CRediT authorship contribution statement

Carolin Hübner: Conceptualization, Methodology, Software, Investigation, Formal analysis, Data curation, Writing - original draft, Visualization. **Alexander C. Schütz:** Conceptualization, Methodology, Supervision, Resources, Writing - review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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Study IV

Rapid visual adaptation persists across saccades

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Keywords: luminance adaptation; perceptual fading; saccadic eye movements; transsaccadic perception

Summary

Neurons in visual cortex quickly adapt to constant visual stimulation, which should lead to perceptual fading within a few tens of milliseconds. However, perceptual fading is rarely observed in every day perception, which may be due to eye movements refreshing retinal input. Recently, it has been suggested that the amplitudes of large saccadic eye movements are scaled to maximally decorrelate the pre- and postsaccadic inputs and thus serve to annul perceptual fading. However, this argument builds on the assumption that adaptation within naturally brief fixation durations is strong enough to survive any visually disruptive saccade and affect perception. We tested this assumption by measuring the effect of short-term luminance adaptation on postsaccadic contrast perception. We found that postsaccadic contrast perception was affected by presaccadic luminance stimulation adapted to over brief periods of fixation. This adaptation effect emerged even within 100 milliseconds and could persist over seconds. These results indicate that adaptation during natural fixation periods can affect perception even after visually disruptive saccades.

Introduction

Humans frequently accelerate their eyes to extremely high velocities (Bahill et al., 1975; Baloh et al., 1975) even though such saccadic eye movements disrupt and distort visual processing (for review see Binda & Morrone, 2018). Nevertheless, humans make saccades about 2 to 4 times per second (e.g. Otero-Millan et al., 2013). What is the advantage of this behaviour? A compelling reason for making saccades is the need to explore a visual scene and to investigate several points of interest with high visual resolution and within a reasonable time. To achieve this, humans quickly shift their fovea towards visual information they detected in the periphery. The fovea is a small central area of the retina densely packed with cone photoreceptors providing the basis for a high-resolution percept at the centre of the visual field. In the peripheral visual field, visual acuity and contrast sensitivity decreases (for review on peripheral vision, see Rosenholtz, 2016; for review on foveal and peripheral interactions, see Stewart et al., 2020). For some animals, which lack a fovea (receptor density is uniform across the retina), making saccades would have no effect considering that the resolution of the visual information would stay the same. The fact that those animals nonetheless make saccades leads to a second potential reason for why humans and other animals frequently interrupt fixations: avoiding perceptual fading due to unchanging retinal input over time, i.e., neuronal adaptation (Samonds et al., 2018). Neuronal adaptation is referred to as the decrease in spiking activity of neurons due to prolonged exposure to an unchanging, redundant input. Perceived contrast of an unchanging visual input will decrease with the reduced spiking activity in the neuronal population (Movshon &

Lennie, 1979) and eventually, it will be erased from vision (perceptual fading, Troxler, 1804). While visual adaptation starts within tens of milliseconds (Müller et al., 1999), perceptual fading takes typically a few hundreds of milliseconds to several seconds (Riggs et al., 1953). However, not only a complete disappearance of visual input is detrimental for perception; the rapid reduction in perceived contrast (Foley & Boynton, 1993; Pavan et al., 2012) of relevant information is already something to avoid for efficient use of vision, which can be achieved by changing the retinal input frequently. The degree of change between inputs determines the degree of improved perceived contrast. Saccades are likely to achieve a large change between successive inputs when shifting gaze positions across distances outreaching the size of the fovea (Otero-Millan et al., 2013). However, Samonds et al. (2018) proposed that the distance that the eyes travel when a saccade is executed (saccade amplitude) is specifically optimised to maximize the change between pre- and postsaccadic inputs (i.e. to decorrelate both inputs). The authors proposed that preferred saccade amplitudes are based on the spatial properties of the visual scene (spatial frequency content) and the sizes of the areas from which neurons process information (receptive filed sizes).

Here we ask the question whether this optimisation of saccade amplitudes is necessary for perception. It might be that a saccade of any (larger) amplitude can induce a visual change that is sufficient to counteract neuronal adaptation. Adaptation may be rapid enough to affect perception within the range of typical fixation durations (Foley & Boynton, 1993; Pavan et al., 2012) but it is certainly weak given short fixation durations compared to prolonged fixations. This weak short-term adaptation might be easily counteracted by the dramatic changes that accompany saccades, for example by the motion streaks caused by the rapid movement of the eyes (Burr & Ross, 1982), which may be so disruptive that they are suppressed (to some extent probably actively) from conscious perception (for reviews, see Ross et al., 2001; Ibbotson & Krekelberg, 2011; Binda & Morrone, 2018). Indeed, the retinal input caused by a saccade-like motion has been shown to strongly alter spiking activity of retinal ganglion cells (e.g. Roska & Werblin, 2003; Idrees et al., 2020), and it is known that simple on- and off flashing of a stimulus (attempting to imitate the effect of saccades) can delay its perceptual fading (Cornsweet, 1956; Bachy & Zaidi, 2014). However, it has been shown that unnaturally long adaptation (≥ 3 seconds) can survive a saccade and influence perception in humans (e.g., Melcher, 2005, 2007; Knapen et al., 2010; He et al., 2018), and that more natural short-term adaptation can attenuate contrast sensitivity and V1 activity across saccades in macaque monkeys (Gawne & Woods, 2003; Niemeyer & Paradiso, 2017). Hence, it is still an open question whether rapid adaptation can be strong enough to affect human perception across saccades as well.

Results

With the present study we address this question by applying a highly sensitive, novel variant of the contrast-cancellation method (Kelly & Martinez-Uriegas, 1993) in which perception of a maximal change (anticorrelated inputs) can be directly compared to that of a minimal/no change (correlated inputs) between inputs from before (pre-) and after a saccade (postsaccadic). Participants saw two adaptation gratings before and two test gratings after a horizontal saccade. They had to discriminate the contrast of the two postsaccadic gratings, one of which was correlated and one anticorrelated to the their respective presaccadic grating due to the new gaze position (for a demonstration see Figure 1). Specifically, a presaccadic fixation stimulus was positioned at the centre of the screen (during adaptation phase) and the position of the postsaccadic fixation stimulus (saccade target), which appeared after about 1.5 seconds, was shifted horizontally (left or right) from the centre by twice the wavelength of one of the gratings (*correlated* grating, $F_{corr} = 2$) which always corresponded to 1.5 or 2.5 times the wavelength of the other grating (*anticorrelated* grating, $F_{anti} = 1.5$ or 2.5. To avoid any undesired built-up of adaptation across trials, multiple properties of the stimuli were randomized across trials: the correlated and the anti-correlated grating were randomly assigned to the top and bottom location, the wavelength of the correlated grating and hence the eccentricity of the postsaccadic fixation stimulus was randomly jittered between ±5° and ±6.35° of visual angle (eccentricity: ±10° to ±12.5°) and the phase of the stimuli was chosen randomly. Provided that participants fixated both fixation stimuli accurately in a trial (we excluded trials in which fixation accuracy was not sufficient, for further details see methods), a participant's postsaccadic retinal input for one half of the screen was replaced by an identical luminance pattern (white stays white and black stays black), and the other half was replaced by a luminance pattern of opposite phase (white becomes black and vice versa). After a subsequent mask stimulus (Figure 2A), participants had to indicate which of the two postsaccadic gratings had the higher contrast (upper or lower).

If the presaccadic fixation duration is sufficient for perceptual adaptation effects to emerge and outlive a saccade, contrast judgements comparing both halves of the screen during the postsaccadic test phase should reveal that a higher contrast of the correlated grating is needed to perceive the contrasts of both gratings as being equal. This would be indicated by a shift in the point of subjective equality (PSE, 50% "anticorrelated-grating-higher" judgements) to negative contrast difference levels Δc ($\Delta c = c_{anti} - c_{corr}$), which we estimated from fitting psychometric functions to repeated contrast discrimination judgements on various levels of contrast differences (Figure 2B).

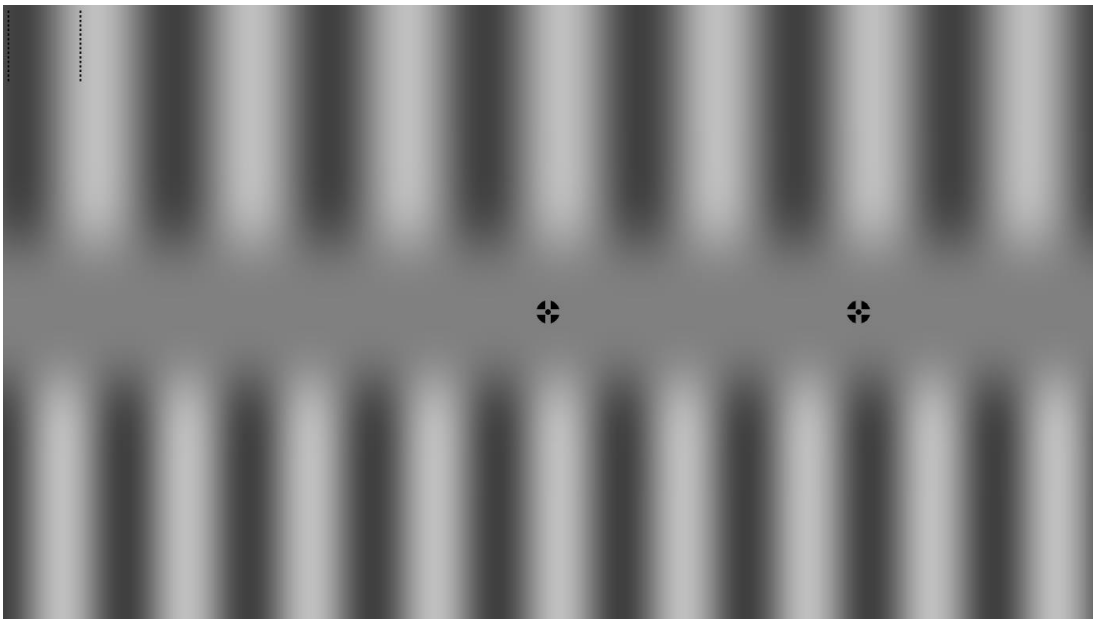

Figure 1. Demonstration of manipulation. *To reproduce appropriate spatial frequencies, one should view the image approximately at a distance of an arms lengths and adjust the size of the image such that one's thumb placed on the image fits approximately in between the two dashed lines in the top left corner of the image. The described effect can be experienced by steadily fixating the central fixation stimulus for a few seconds, or (to achieve the largest possible effect) until the gratings begin to fade, and subsequently saccade towards the second fixation stimulus to the right. While fixating the second fixation stimulus, one should observe the top-half grating to be of lower contrast (correlated grating) than the bottom-half grating (anticorrelated grating). When the second fixation stimulus is fixated steadily, with low variance in gaze position, the effect can be observed for a long time.*

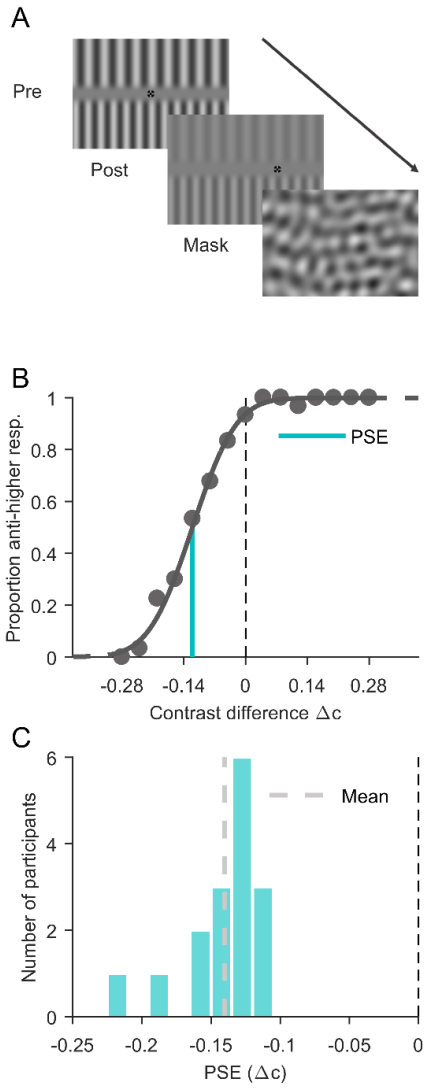

Figure 2. Trial procedure and main adaptation effect (Experiment 1). *(A) The sequence of presaccadic- (adaptation phase, until saccade onset), postsaccadic- (test phase, 400ms duration) and mask (300ms duration) stimuli seen by a participant during a trial. The arrow indicates direction of time. Fixation stimuli are not drawn to scale. (B) Example psychometric function fitted to proportion anticorrelated-grating-higher responses over contrast differences Δc illustrating a point-of-subjective-equality (PSE) shift away from zero towards a negative contrast difference level (distance between dashed and turquoise line). A negative PSE indicates a higher perceived contrast of the anticorrelated grating. (C) Histogram of PSEs in contrast difference for all participants. The light-grey dashed line represents the mean PSE. The black dashed line represents a PSE of zero expected for unbiased responses.*

Experiment 1: Strong and robust adaptation

Average median saccade latency (time until saccade initiation after saccade target onset) over participants was 191 ± 39 ms (mean ± standard deviation) leading to a mean adaptation duration of 1705 ± 38 ms for Experiment 1. We found strong PSE shifts towards negative contrast differences (Figure 2C), indicating that the correlated grating needed to be higher in contrast by 0.14 ± 0.03 Δc, for both gratings to be perceived as equal (one-sided t-test against zero: $t(15) = -21.02$, $p < 0.0001$). This means that we found robust perceptual adaptation effects, which persisted from one fixation to a next across a saccade.

Experiment 2: Rapidly emerging adaptation

In the second experiment, we went on to test the limits of this effect and whether it can emerge within more natural fixation durations of a few hundred milliseconds. Here, only one contrast difference level (-0.07) was tested and the adaptation duration varied in the range of 16 ms to 1,384 ms, which was partially dependent on the participants saccade latency in a given trial. For instance, if in a trial we intended a 100ms adaptation duration this would often be shorter than a typical saccade latency. Therefore, we estimated a participant's median saccade latency from previous trials and the adaptation stimulus would only be shown 100 ms before the predicted saccade onset (for further details see Methods). The average median saccade latency was 169 ± 23 ms and the aggregated number of valid trials over all 100ms bins (Figure 3A) averaged over participants was 26 ± 12. The proportion of responses indicating that the anticorrelated grating was perceived as of higher contrast (despite the fact that it had a physically lower contrast) increased with increasing adaptation durations (Figure 3B); and importantly, was already significantly higher for the shortest adaptation durations tested (0.39 ± 0.09 for durations ≤ 100ms), than the estimated baseline (0.17 ± 0.07 estimated from the fits in Experiment 1 when PSEs were set to zero; two-sample t-test: $t(21) = 6.55$, $p < 0.0001$).

Experiment 3: Persistent adaptation

As the effect showed to be strong, robust, and rapidly emerging, we tested in a third experiment for how long it would persist when we inserted delays (blank-screen period) between adaptation and test phase of various lengths. The experiment was identical to the main experiment (Experiment 1), except the screen was blanked upon saccade detection for a certain period (100 to 1600 ms) and some minor changes in the timing of the adaptation and the fixation stimulus (for further details see methods). Average median saccade latency was 159 ± 24 ms and mean adaptation duration was 1505 ± 3 ms for Experiment 3. PSE shifts decreased with blank durations and followed a logarithmic function starting at a PSE of -0.12 ± 0.04 Δc for no delay and reaching -0.06 ± 0.02 Δc for a delay of 1.6 seconds (Figure 3C). Since even the PSE for longest delay was significantly below zero (one-sample t-test against zero: $t(6) = -11.24$, $p < 0.0001$), these results indicate that the adaptation effect was also extremely persistent over time.

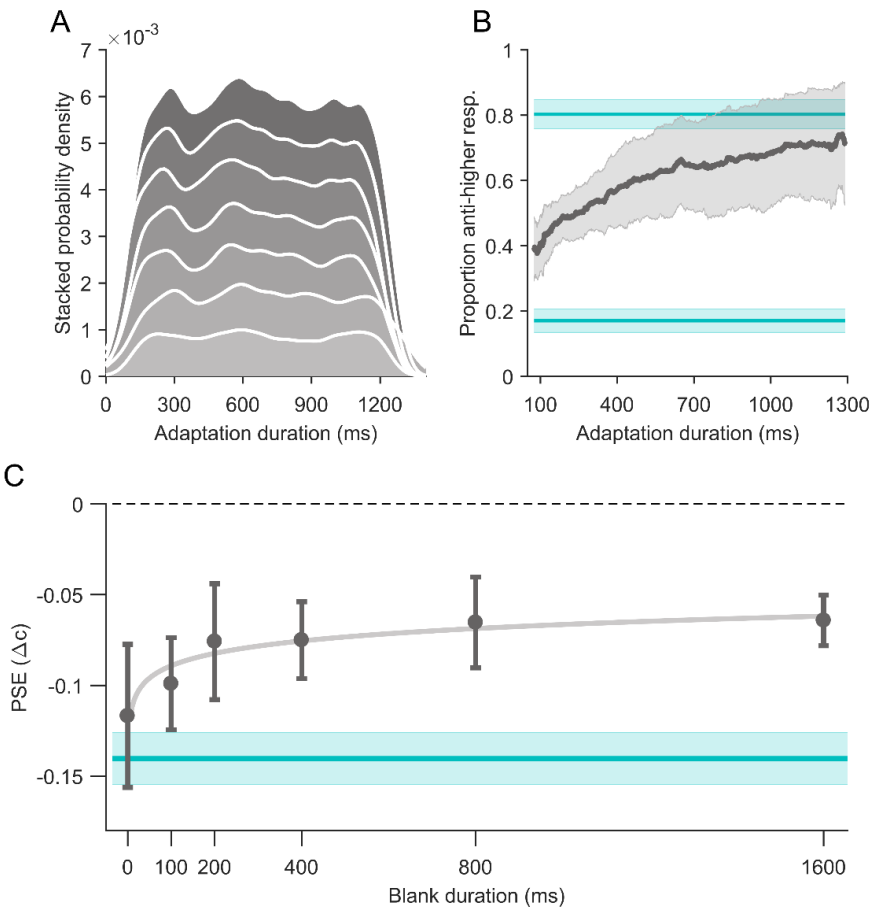

Figure 3. Results for build-up (Experiment 2) and decay (Experiment 3) of adaptation. *(A) Stacked probability density plot of number of valid trials over adaptation durations tested for seven participants in Experiment 2. Absolute number of trials can be found in* ***Error! Reference source not found.****. (B) Results testing the build-up of the adaptation effect over time in Experiment 2. Proportion of responses for perceiving the anticorrelated grating as of higher contrast over adaptation duration in milliseconds. The dark-grey line represents the mean proportion over participants and the light-grey area its 95%-confidence interval. The upper turquoise line represents the expected mean proportion of responses given the average PSE from the Experiment 1. Likewise, the lower turquoise line represents the expected mean proportion of responses under the assumption of a PSE of zero (indicating no adaptation effect). The shaded area of both lines represents their 95%-confidence interval. (C) Results testing persistence of the adaptation effect over time in Experiment 3. PSE values in contrast difference over postsaccadic blank duration in milliseconds. Dots represent means across participants and error bars the 95%-confidence interval. The light-grey solid line represents the logarithmic function fitted to the mean data. The black dashed line at zero indicates the PSE value expected for no adaptation effect. The turquoise*

line (mean) and shaded area (95%-confidence interval) represent aggregated PSE values from Experiment 1.

Experiment 4: Stronger adaptation around the centre of gaze

To investigate whether the observed adaptation effect was primarily driven by adaptation around the centre of gaze or in the periphery, we tested a separate group of participants with a similar paradigm to Experiment 1, with the only difference being that the postsaccadic test stimuli were reduced to only a vertical slice of both gratings (a noise mask covered the rest of the gratings) positioned either around the centre of gaze at the saccade target position (central condition) or in the periphery at the presaccadic fixation position (peripheral condition, Figure 4A). Average median saccade latency was 219 ± 64 ms for the central condition and 234 ± 80 ms for the peripheral condition leading to a mean adaptation duration of 1724 ± 62 ms for the central condition and 1742 ± 73 ms for the peripheral condition. Negative PSE shifts (Figure 4B) show an effect of adaptation around the centre of gaze (-0.11 ± 0.03 Δc; $t(5) = -8.96$, $p < 0.001$) and in the periphery (-0.03 ± 0.02 Δc; $t(5) = -4.09$, $p = 0.009$); and the adaptation effect was significantly stronger around the centre of gaze compared to the periphery ($t(5) = -6.48$, $p = 0.001$). This difference cannot be due to a lower discrimination performance in the periphery as JNDs (Figure 4C) were approximately equal for both conditions ($t(5) = -0.14$, $p = 0.898$). The results indicate that the PSE shifts from a central and peripheral part of the visual field almost perfectly add up to the PSE shift observed with a full test stimulus in Experiment 1 (-0.14 ± 0.03 Δc) and that a large portion of the adaptation effect is driven by the area around the centre of gaze.

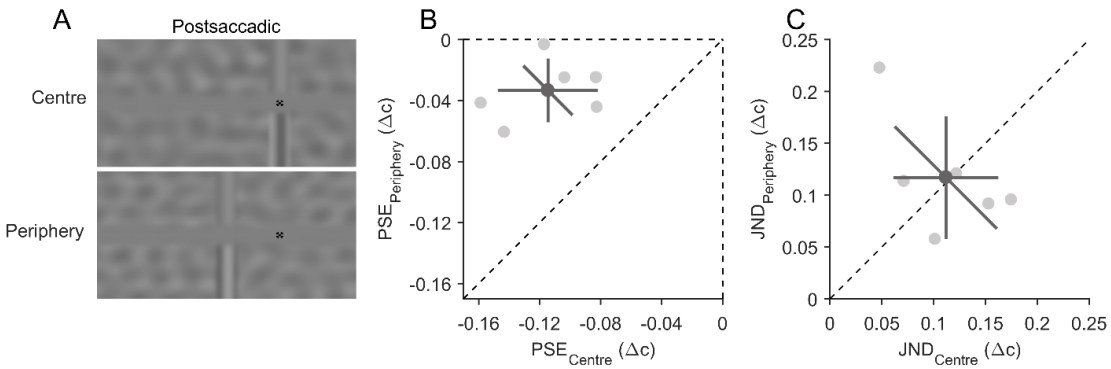

Figure 4. Test stimuli and results for contribution of visual field (Experiment 4). A) *Example postsaccadic test displays presented to a participant in Experiment 4 for when the test-stimulus slice was presented around the centre of gaze (upper panel) or to the periphery (lower panel). Fixation stimuli are not drawn to scale.* ***B)*** *Scatter plot for all points of subjective equality (PSE) compared between the central condition (horizontal axis) and peripheral condition (vertical axis). Data points above the dashed vertical line indicate a stronger adaptation effect for when the test-stimulus slice was presented around the centre of gaze.* ***C)*** *Scatter plot for just-noticeable differences (JNDs) compared between the central condition (horizontal axis) and peripheral condition (vertical axis). Data points on the diagonal dashed line indicate that participants were equally precise in both conditions.* ***B-C)*** *Light-grey dots represent individual participant data and the dark-grey dot indicates the overall mean. The*

error bars indicate 95%-confidence intervals within each condition (cardinal bars) or between conditions (oblique bar).

Discussion

By comparing the perceived contrast of two postsaccadic gratings of which one was correlated and one was anticorrelated with the presaccadic retinal input, we found that short-term perceptual adaptation survives saccades, that it can build-up rapidly between saccades within the typical duration of fixations and that it can last for more than one second. When we reduced postsaccadic test stimuli to either a central or peripheral part of the visual field, we found that the observed adaptation effect was predominantly driven by the visual field around the centre of gaze position.

Implications for natural fixation behaviour

Given this time course for build-up and decay of the perceptual effect, we conclude that perceptual fading due to correlations between pre- and postsaccadic inputs can have dramatic consequences for vision, and that neuronal activation or refresh due to retinal smear (Burr & Ross, 1982) or saccadic suppression of contrast sensitivity (for reviews, see Ross et al., 2001; Ibbotson & Krekelberg, 2011; Binda & Morrone, 2018) is not sufficient to washout short-term adaptation. Some authors argued that adaptation within natural fixation durations would be too weak or short-lived to affect perception (e.g., Poletti & Rucci, 2016). However, previous (Foley & Boynton, 1993; Pavan et al., 2012) and our perceptual results suggest that adaptation is not merely a challenge for prolonged fixations, but also for the typical fixation durations of 200 – 300 ms that occur during natural exploration (Wilming et al., 2017).

Classic studies on the time course of neuronal adaptation (e.g. Müller et al., 1999) did not take into account the effect of fixational eye movements – such as microsaccades and ocular drift, which can delay perceptual fading by introducing small changes to the retinal input during fixation (Martinez-Conde et al., 2004). The role of fixational eye movements in counteracting perceptual fading is however strongly debated (for review see Poletti & Rucci, 2016). Specifically in our study, their role might be negligible due to the low spatial frequencies of the gratings (Tulunay-Keesey, 1982). As microsaccade amplitudes are in the range of 0.05° to 0.5° of visual angle (Poletti & Rucci, 2016), they are by definition not large enough to induce considerable changes to the retinal input given our low spatial frequency stimuli (minimal bar width = 2°). In general, small fixational eye movements should only decorrelate inputs on a correspondingly small spatial scale, i.e. in the high spatial frequency range, whereas large saccades decorrelate also in the low spatial frequency range. We have exclusively used low spatial frequencies (0.12 - 0.25 cyc/°) in our stimuli to make the intended manipulation work: full correlation or anticorrelation between retinal inputs across saccades could not be achieved if participants made saccadic landing errors, which they usually do but in a predictable range of 0.5° to

1° of visual angle for larger horizontal saccades as used here (on average 11.25°; van Opstal & van Gisbergen, 1989). The lower spatial frequencies i.e., the large bar widths in our gratings offer a larger tolerance for saccade landing errors and hence enabled us to reduce the expected number of invalid trials. While the low spatial frequencies made this manipulation feasible, low spatial frequencies also typically dominate natural scenes (Burton & Moorhead, 1987; Field, 1987; Ruderman & Bialek, 1994) and the combination of contrast and spatial frequencies we used in the adaptation stimulus is comparable to skies or grounds in natural-scene images (Frazor & Geisler, 2006; see also Figure S2). As natural stimuli nevertheless consist of a variety of spatial frequencies and orientations, a high degree of- but not necessarily a full correlation is likely to occur between consecutive fixations.

Decorrelation of inputs as explicit purpose of saccades

It may still be discussed whether the perceptual refresh due to a large saccade is a coincidental by-product rather than based on accurate evaluation of spatial properties of a natural scene as suggested by Samonds et al. (2018), and that the latter would only apply if there is no superior goal that leads the saccade such as bringing a target of interest into the fovea. That counteracting perceptual fading is a by-product rather than a purpose has been proposed for fixational eye movements given that microsaccade- or drift rates did not increase (rather decrease) with advancing perceptual fading (Cornsweet, 1956; Poletti & Rucci, 2010). The purpose of fixational eye movements may exclusively be increasing the precision of fixations (Cornsweet, 1956; Poletti & Rucci, 2010) and such enhancing the perception of fine spatial detail (e.g. Rucci et al., 2007; Rucci & Desbordes, 2003). Placing the fovea onto a region of interest might in turn be the behaviourally most relevant function for large saccades; but it is likely also a more modern function in evolutionary terms. For example, many fish make saccades despite not having a fovea to place a target at for detailed inspection and do not show saccade behaviour specific to target inspection (for review see Land, 2019). In addition, Samonds et al. (2018) could show that saccade amplitudes in afoveate mice scale with their visual acuity (upper limit of spatial frequency range obtainable) during passive viewing. Importantly, human saccade- and fixation behaviour in passive viewing depend on spatial properties of the scene consistent with the decorrelation hypothesis: Groner and colleagues (2008) demonstrated that human saccade amplitudes become larger when inspecting natural images with increased low spatial frequency content compared to high spatial frequency content. In addition, Mostofi et al. (2020) showed that saccades reduce redundant luminance information (i.e. the power of low spatial frequencies) obtainable from natural scenes over time when the scene is passively explored. Krieger et al. (2000) could show that regions with higher spatial variance (higher potential to lead to decorrelation) were more likely to be fixated. In addition, patches of decorrelated input in the visual field are likely to attract gaze orienting (Ludwig et al., 2012). In conclusion, perceptual refresh may not be the primary

function of saccades in daily vision but likely one in passive viewing and a more deep-rooted function in general, as it is based on fundamental neuronal properties.

Neuronal locus of the perceptual adaptation effect

Adaptation is a ubiquitous neuronal property inherent to every processing level in the visual hierarchy (for reviews, see Kohn, 2007; Webster, 2015) and rapid adaptation in lower-level visual areas can be passed on to higher-level visual areas and affect behaviour (Jin & Glickfeld, 2020). As the adaptation effect we measured is retinotopic and specific to the phase of the gratings, the neuronal locus for this effect should not go beyond simple cells (Hubel & Wiesel, 1962), in the primary visual cortex (V1) because processing is phase-invariant in complex cells and at higher processing levels. At the lower end, it could have its origin as early as in the bleaching of cone photoreceptors. Negative afterimages resulting from mid-photopic stimulation (such as here) should, however, have their origin in the adaptation of retinal ganglion cells (Zaidi et al., 2012). Given that we found a stronger adaptation effect in the central visual field compared to the periphery, and that an adapted state itself does not remap across saccades (He et al., 2018), one could conclude that the observed proportional contributions to the adaptation effect are related to the varying density of ganglion cells across the visual field, which decreases with increasing eccentricity (Wässle et al., 1990).

Conclusion

We show that luminance adaptation can be strong, rapid, and persistent enough to attenuate contrast perception within natural fixation durations, and that this effect can outlast a large saccade despite the strong disruption of visual input. Our findings indicate that attenuation of postsaccadic contrast can indeed be a relevant issue for human perception and that therefore, decorrelation of retinal inputs might be a plausible objective to constrain the range of potential saccade amplitudes (Samonds et al., 2018).

Limitations of the Study

To investigate the possibility of short-term adaptation to affect perception we aimed to make the effect as visible as possible by 1) letting participants compare a correlated and an anticorrelated grating, and 2) by using a lower mean contrast of the postsaccadic test stimuli. Regarding the first point, many previous studies either investigated adaptation effects on the perception of a single correlated stimulus (e.g., Kelly & Martinez-Uriegas, 1993) or on the removal of the adapted stimulus to investigate the perception of afterimages (e.g., Tulunay-Keesey, 1982). In comparison to these methods, our method might give us an upper bound of the effect as we did not measure the reduction (correlation) and increase (decorrelation) in perceived contrast separately, but measured the difference between the perceived contrast of correlated and anticorrelated stimuli. Regarding the

second point, we conducted a version of Experiment 1 where the mean contrast of the test stimuli was as high as the contrast of the adaptation stimuli (see Supporting Experiment). The effect was smaller but nevertheless robust and significantly different from zero. However, also in this version we used an adaptation duration that is brief compared to most adaptation studies but still exceeding typical fixation durations. The effect is likely to diminish with a reduced adaptation duration as indicated by the results of Experiment 2. While it is hence arguable that an adaptation effect due to correlations between pre- and postsaccadic inputs might be noticeable under more natural conditions, we see our study as proof of principle and are convinced that even a very small attenuation of perceived contrast may matter to the visual system.

STAR Methods

Resource Availability

Lead Contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Alexander C. Schütz (a.schuetz@uni-marburg.de).

Materials Availability

This study did not generate new specimens or materials. All images are included in the text and Supporting Information.

Data and Code Availability

Eye-movement data and log-files will be made publicly available at zenodo, doi: 10.5281/zenodo.4568210.

Experimental Model and Subject Details

In Experiment 1, we tested twenty participants who were unaware of the purpose of the study. Three of them discontinued the experiment before a sufficient number of trials for analysis was completed. Another participant was excluded from further analysis after data inspection revealed that the participant misinterpreted the experimental task (gratings discriminated by spatial frequency instead of contrast). The data of sixteen participants (12 female, 4 male; mean age = 22 years, range = 18-27 years) was used for analysis. In Experiment 2 and 3, six participants who were unaware of the purpose of the study and one author (CH) were tested and included into analysis (5 female, 2 male; mean age = 25 years, range = 22-33 years). In Experiment 4, we tested and included six participants who were unaware of the purpose of the study (5 female, 1 male; mean age = 23 years, range = 22-24 years). For the Supporting Experiment, three participants unaware of the purpose of the experiment and one of the authors (4 female; mean age = 25 years, range = 22-29 years) were tested and included into

analysis. All participants were either students or associates of Marburg University, had normal or corrected-to-normal vision, and gave informed consent prior participation. The study was conducted in accordance with the principles of the Declaration of Helsinki 1964 and authorized by the local ethics committee of the psychology department at Marburg University (proposal number 2015-35k).

Method Details

Stimuli

The horizontal grey bar separating the upper and lower luminance gratings in adaptation- and test phase was created by applying a one-dimensional, generalised gaussian (inversed) window (scale α = 2.1° of visual angle, shape β = 3) elongated to the length of the display. By this, the edges of the grey bar blend into the gratings and the centre of the bar is fully oblique. Pre- and postsaccadic fixation stimuli were black and a combination of a bull's-eye and crosshair (Thaler et al., 2013) with a diameter of 0.6°. The wavelength of the correlated grating was chosen randomly between 5° and 6.25° (spatial frequency: 0.16 to 0.2 cyc/°). The wavelength of the anticorrelated grating (λ_{anti}) fulfils the equation $\lambda_{anti} = \frac{(\lambda_{corr}*2)}{F_{anti}}$, with the factor F_{anti} being either 1.5 or 2.5. Hence, the wavelength of the anticorrelated grating varied between 4° and 8.3° (spatial frequency: 0.12 to 0.25 cyc/°). The common phase of the two gratings was jittered randomly between -0.5 π and 0.5 π. While the spatial properties of the gratings remained the same for adaptation and test phase, contrast was differing. The contrast of the adaptation stimulus (both gratings before saccade) was 0.5. The constant mean contrast level of the test stimulus (both gratings after saccade) was 0.15 (the mean contrasts were different in the Supporting Experiment, see Design). A mask stimulus following the test stimulus covered the entire screen with Gaussian-filtered white noise with an average spatial frequency of 0.18 ± 0.02 cyc/° and a contrast of 0.7. The test stimuli of Experiment 4 (Figure 4A) differed from the test stimuli of Experiments 1-3 by the following: both gratings were covered by a mask stimulus that included a vertical generalised gaussian window (α = 2.1°, β = 5). This window uncovered a slice of the gratings and its centre was positioned either at the postsaccadic target location (central condition) or at the screen centre (peripheral condition).

Equipment

Stimuli were displayed on a VIEWPixx monitor in M16 mode (greyscale) at a 1920×1080-pixel resolution and a 120-Hz refresh rate. The display had a size of 51.5×29 cm and was viewed at a distance of 60 cm. Luminance was 0.21 cd/m² for black, 105.70 cd/m² for white, and 58.33 cd/m² for grey pixels. Eye movements were recorded with a desktop-mounted EyeLink 1000 (SR Research Ltd., Ontario, Canada) with a sampling rate of 1000 Hz. Experimental software and analysis were written in MATLAB R2017a (Mathworks, Natick, MA, USA) using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) for stimulus display and the Eyelink Toolbox (Cornelissen et al., 2002) for eye tracker operation.

Participants responded using a standard keyboard. Participant's head position was stabilised using a forehead- and chinrest.

Design

For Experiment 1 and 4, the contrast difference between the anticorrelated- and the correlated grating took on values from minus and plus 0.28 in steps of 0.04, with negative values indicating a higher contrast of the correlated grating. In Experiment 2, only one contrast difference of -0.07 was tested. In Experiment 3, tested contrast differences ranged between -0.3 and 0.2 in steps of 0.05. The method of constant stimuli (Fechner, 1860) was used in Experiment 1, 3, 4, and the Supporting Experiment to obtain psychometric functions. Contrast differences, the position of the correlated- and anticorrelated gratings (upper or lower half) and the value of F_{anti}, and the conditions in Experiment 2 (intended adaptation duration: 100-1200 ms in 100ms steps) and 3 (postsaccadic blank duration: 0, 100, 200, 400, 800, and 1600 ms), were counterbalanced and trial order was randomised. In Experiment 4, the two conditions (location of slice: centre, periphery) were blocked (block order was counterbalanced across participants) and within each block contrast differences, grating position, and value of F were counterbalanced and trial order was randomised. Each factor combination was measured at least 8 times in Experiment 1 and 3 resulting in 480 and 528 trials respectively, four times in Experiment 2 resulting in 384 trials, and two times in Experiment 4, resulting in 120 trials per block. The Supporting Experiment was similar to Experiment 1 with the differences that the contrast of the adaptation stimulus was randomly jittered between 0.3 and 0.7 across trials, that the overall contrast of the test stimulus was equal to that of the adaptation stimulus, and that there was no mask following the test stimulus. Contrast difference levels tested in the Supporting Experiment were -0.4, -0.3, -0.2, -0.15, -0.1, -0.05, 0, 0.05, 0.1, 0.15, 0.2, 0.3, 0.4.

Eye-tracker calibration

The eye tracker was calibrated using the participant's right eye, for 9 locations (marked by a fixation stimulus) in a grid array with one location at the centre of the screen and the remaining with an eccentricity of 13° of visual angle on the horizontal and/or 5° on the vertical axis. The experimenter confirmed gaze position at each location manually, while ensuring that each difference between computed gaze position and stimulus location was below 0.5° and below 0.35° on average during validation. The calibration procedure was conducted before the start of each experiment, and after every 100 trials. In addition to the calibration procedure, at the start of each trial a drift correction was implemented, that was manually confirmed by the participant using the space bar on the keyboard.

Procedure

Participants started each trial by pressing the space bar while fixating a central fixation. In Experiment 1, 4, and the Supporting Experiment the adaptation stimuli were displayed upon trial initiation and the saccade target (also postsaccadic fixation stimulus) was added at an eccentricity of twice the wavelength of the correlated grating to the left or right (between ±10° and ±12.5°) after a duration

chosen at random between 1.4 and 1.6 s. The central fixation stimulus disappeared after an additional 200 ms or when a saccade was detected (overlap paradigm, Saslow, 1967). A saccade was detected when the recorded gaze position exceeded 2° of visual angle in respect to screen centre. Upon saccade detection, the adaptation stimulus was replaced by the test stimulus, which was 400ms later replaced by a mask (the Supporting Experiment did not have a mask but the screen turned grey after 400 ms). After an additional 300 ms the screen turned grey, which prompted the participants to respond by pressing the up-arrow key for reporting to have perceived the upper half as of higher contrast or the down-arrow key for reporting to have perceived the lower half as of higher contrast. Auditory feedback was given after each trial for inaccurate fixation- or saccade behaviour towards the pre- or postsaccadic fixation stimulus position.

The procedure of Experiment 2 differed from the procedure of Experiment 1 by the following: the central fixation stimulus disappeared upon onset of the saccade target (no overlap paradigm, note that the adaptation stimulus i.e., the gratings, are distinct from the fixation stimuli) and the onset of the saccade target was fixed in time to 1.2 s after trial initiation. To enable very short adaptation durations (e.g., 100 ms), and assuming that adaptation continues during saccade preparation, the saccade latency of the participant was estimated by taking the median saccade latency of the previous 20 trials available. The saccade-latency estimate for the first trial was set to 190 ms. If the estimated saccade latency on a given trial was equal to the intended adaptation duration, saccade target and adaptation stimulus were displayed simultaneously (preceded by 1.2 s of grey screen and the central fixation stimulus). If the estimated saccade latency was longer than the intended adaptation duration, the onset of the saccade target was followed by the onset of the adaptation stimulus by the respective time difference. The order was reversed when the estimated saccade latency was shorter than the intended adaptation duration i.e., the onset of the adaptation stimulus preceded the onset of the saccade target. As in Experiment 1, the adaptation stimulus was replaced by the test stimulus upon saccade detection.

Saccade latency in Experiment 3 was estimated in the same way as in Experiment 2. One purpose here was to ensure a relatively constant adaptation duration within and across participants of 1.5 s. That is, the onset of the adaptation stimulus after trial initiation was delayed by the estimated saccade latency and saccade target onset was set to 1.5 s after trial initiation. The central fixation stimulus disappeared upon saccade target onset (no overlap paradigm). The adaptation stimulus disappeared upon saccade detection and the subsequent onset of the test stimulus was delayed by the intended blank duration. In all remaining aspects the procedure of Experiment 3 was similar to that of Experiment 1.

Trial exclusions

Single trials were excluded from analysis based on participant's fixation accuracy in adaptation- and test phase as the position of gaze with respect to the gratings was crucial to our manipulation. For all experiments, we excluded trials which contained blinks in the time between trial initiation and mask onset, trials in which the switch between adaptation- and test stimuli was not achieved in the time of the saccade (e.g. due to small, consecutive saccades instead of one large saccade), and trials in which the standard deviation of horizontal gaze positions sampled between adaptation-stimulus onset and saccade onset was above 0.5°. The latter was to ensure a stable gaze position during the adaptation phase. Horizontal saccade amplitude led to trial exclusion based on the ratio of saccade amplitude and correlated-grating wavelength ($F_{corr} = Ampl/\lambda_{corr}$) and the absolute difference to its nearest natural number. A difference of 0.5 is the worst possible outcome in respect to our manipulation, as this would mean that the participant's saccade amplitude inverted the characteristics of the two gratings (correlated became anticorrelated grating and vice versa). A difference of zero corresponds to the best-case scenario. We excluded all trials in which the difference was equal to or above the boundary between best and worst case of 0.25.

In addition to the exclusion criteria common to all experiments, we excluded trials of Experiment 1, 4 and the Supporting Experiment in which the saccade latency was above 600 ms (< 1 % of trials), and trials of Experiment 3 in which the adaptation duration deviated more than 100 ms from the intended adaptation duration of 1.5 s (6 ± 5 % of trials). Total amount of trials excluded was 9 ± 9 % for Experiment 1, 9 ± 5 % for Experiment 2, 7 ± 6 % for Experiment 3, 2 ± 3 % (central condition) and 8 ± 12 % (peripheral condition) for Experiment 4, and 19 ± 18 % of trials For the Supporting Experiment.

Quantification and Statistical Analysis

Eye-movement data analysis

For eye-movement data analysis saccades were detected offline using the EyeLink 1000 algorithm (velocity threshold = 22°/s, acceleration threshold = 3800°/s²). Saccade onsets were defined as the first sample after saccade-target onset in which a saccade was detected; likewise, saccade offsets were defined as the last sample after saccade onset in which a saccade was detected. Presaccadic fixation position was defined as the mean of all gaze positions sampled between adaptation-stimulus onset and saccade onset. Postsaccadic fixation position was defined as the mean of gaze positions sampled between saccade offset and mask onset, during the time the test stimulus was presented. Saccade amplitude was defined as the difference between post- and presaccadic fixation position. Saccade latency was defined as the time (resolution of 1 ms) between saccade-target onset and saccade onset. Adaptation duration was defined as the time between adaptation-stimuli onset and saccade onset.

Response data analysis

To obtain psychometric functions for Experiments 1, 3, 4, and the Supporting Experiment, perceptual choices were sorted by contrast-higher responses for the anticorrelated grating (anticorrelated-higher responses) and their proportion was calculated for each contrast-difference level tested. A cumulative Gaussian was fitted to the data using psignifit 4.0 toolbox (Schütt et al., 2016). The point of subjective equality (PSE) was estimated as the level of contrast difference corresponding to 50% anticorrelated-higher responses. A negative PSE indicates a perceptual bias for perceiving the correlated grating of lower contrast and the anticorrelated grating of higher contrast. The just-noticeable difference (JND) was defined as the standard deviation of the cumulative Gaussian, with a lower JND indicating higher precision of the contrast discrimination.

For Experiment 2, proportions anticorrelated-higher responses (for the one contrast-difference level tested) were calculated as a running average over all adaptation durations that resulted from the procedure. The adaptation durations reached values between 16 and 1384 ms and the average number of trials per 100ms bin (range 0 – 1400 ms) was 26 ± 2 across participants. The running average was calculated starting from 0 ms in 300ms bins and 1ms steps ending at 1400 ms. The very first bin was only half the bin size (150) and it was increased by 1 until it the full bin size of 300 was reached; until then, every bin's starting point remained at zero milliseconds (0 – 150 ms, 0 – 151 ms, …, 0 – 300 ms). The same procedure but reversed was applied for the end of the range (1100 – 1400 ms, 1101 – 1400 ms, …, 1250 – 1400 ms). The proportion of anticorrelated-higher responses was assigned to the mean of each bin.

For Experiment 3 we fitted a natural logarithm to the PSEs for each participant and for mean PSEs using the implemented log-function in MATLAB and two free parameters A and B following the equation $y = A * log(x) + B$.

All statistical test were made using MATLAB R2017a (Mathworks, Natick, MA, USA) software, and the alpha value was set to 0.05.

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Author Contributions

Conceptualization, Methodology, Software, Investigation, Formal Analysis, Data Curation, Writing – Original Draft, Visualization, C.H.; Conceptualization, Methodology, Supervision, Resources, Writing – Review & Editing, A.C.S.

Declaration of Interests

The authors declare no competing interests.

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Zusammenfassung

Die vorliegende Dissertation widmet sich der Frage, wie das gesunde menschliche Gehirn angesichts der heterogenen und inkohärenten Informationen, die dem visuellen System über seine Umwelt zur Verfügung stehen, homogene und kohärente visuelle Erfahrungen erzeugen kann. Heterogenität bezieht sich auf die unterschiedliche räumliche Auflösung der visuellen Informationsverarbeitung über das gesamte Gesichtsfeld (Fovea bis Peripherie). Inkohärenz bezieht sich auf Verzerrungen und Unterbrechungen des Informationsflusses, die durch schnelle, ruckartige Augenbewegungen namens Sakkaden erzeugt werden. Beide Aspekte und deren Implikationen werden in der Einleitung der vorliegenden Arbeit beschrieben. Die Ansätze und Ergebnisse von vier Studien, die jeweils zum Verständnis des oben genannten Problems der visuellen Stabilität beitragen, werden nachfolgend skizziert.

Um zu verstehen, ob und wie Informationen von vor- und nach einer Unterbrechung durch eine Sakkade in die Wahrnehmung integriert werden, wurde in der ersten Studie (Studie I) untersucht, ob die Wahrnehmung jener Reize durch eine statistisch optimale Integration prä- und post-sakkadischer Signale beschrieben werden kann. Die Ergebnisse zeigten, dass die Wahrnehmungsleistung annähernd den Vorhersagen für eine optimale trans-sakkadische Integration entsprach. Integration schien sogar dann einzutreten, wenn sich im präsentierten Stimulus einige visuelle Eigenschaften während der Sakkade veränderten.

Da das Ergebnis der ersten Studie impliziert, dass die Integration von prä- und post-sakkadischer Information auch über Stimulusveränderungen hinweg ein robustes Phänomen ist, stellte sich die Frage, was zu einer trans-sakkadischen Segregation führen würde, d. h., ab wann eine Stimulusveränderung wahrgenommen werden würde. Angetrieben von dem Gedanken, dass sich die Fähigkeit zur Informations-Integration oder -Segregation über die Lebenspanne entwickelt, zielte die zweite Studie (Studie II) darauf ab, trans-sakkadische Segregation bei Kindern im Vergleich zu jungen Erwachsenen zu untersuchen. Die Studie zeigte, dass Kinder einen Stimulus-Versatz über eine Sakkade hinweg weniger genau erkennen als Erwachsene, was auf eine verminderte Fähigkeit zur trans-sakkadischen Segregation in der Kindheit hinweist. Die Segregationsfähigkeit von Kindern zeigte jedoch eine größere Verbesserung im Vergleich zu Erwachsenen, wenn ein Hilfsreiz eingefügt wurde (post-sakkadische Leerstelle). Darüber hinaus machten Kinder weniger genaue und weniger präzise Sakkaden als Erwachsene, korrigierten aber auch ihren Blickpositionsfehler nach der Sakkadenlandung schneller. Diese Ergebnisse legen nahe, dass sakkadische Unsicherheit (Erwartungshaltung über selbstinduzierte Positionsfehler) eine Rolle bei der trans-sakkadischen Wahrnehmung spielt.

Um die Grundsätze trans-sakkadischer Segregation weiter zu bestimmen, untersuchte die dritte Studie (Studie III) die Wahrnehmung von intra-sakkadischen Formveränderungen (Zunahme oder Abnahme von Kreisförmigkeit), auch im Verhältnis zur unterschiedlichen Form-Wahrnehmung zwischen Fovea und Peripherie. Die Ergebnisse zeigten, dass Formveränderungen, bei denen Objekte über eine Sakkaden hinweg kreisförmiger wurden, besser von den Teilnehmern wahrgenommen werden (als wenn die Objekte eckiger wurden). Darüber hinaus erschien die Form vor einer Sakkade im peripheren Gesichtsfeld kreisförmiger als nach einer Sakkade in der Fovea. Diese Ergebnisse legen die Existenz einer Prädisposition nahe, Formänderungen zu erkennen (Erhöhung der Kreisförmigkeit), die der typischen trans-sakkadischen Erfahrung (Erniedrigung der Kreisförmigkeit) entgegengesetzt sind. Dies untermauert die Vermutung, dass Erwartungen bezüglich typischer trans-sakkadischer Wahrnehmung eine Schlüsselrolle bei der Fähigkeit zur intra-sakkadische Veränderungserkennung spielen.

Die vierte Studie (Studie IV) widmete sich der Frage, wie sich prä-sakkadische visuelle Stimulation auf die post-sakkadische Wahrnehmung auswirkt. Sie untersuchte den Effekt kurzzeitiger Luminanz-Adaptation vor einer Sakkade auf die Kontrastwahrnehmung nach der Sakkade. Die Ergebnisse zeigten, dass die post-sakkadische Wahrnehmung durch prä-sakkadische Adaptation beeinflusst werden kann, sogar, wenn die Adaptation sehr kurzzeitig — auch im Bereich natürlicher Fixierungsdauern — war.

Zusammenfassend lässt sich sagen, dass trans-sakkadische Wahrnehmung durch Integration oder Segregation von prä- und post-sakkadischer Information bestimmt wird. Studie I zeigte, dass eine trans-sakkadische Integration trotz großer intra-sakkadischer Reizveränderungen erfolgen kann. Studien II und III legen nahe, dass die trans-sakkadische Segregation von wiederkehrenden trans-sakkadischen Erfahrungen abhängt. Studie IV zeigte, dass die trans-sakkadische Wahrnehmung wahrscheinlich von grundlegenden Aspekten der visuellen Informationsverarbeitung, wie Adaptation, beeinflusst wird. Zusammenfassend legt diese Dissertation nahe, dass das visuelle System statistisch optimale- und prädiktive Mechanismen für den Strom an heterogenen und inkohärenten Informationen entwickelt hat, um eine kohärente und anpassungsfähige Wahrnehmung der Umwelt zu erzeugen.

Author contributions

Study I: Hübner, C., & Schütz, A. C. (2017). Numerosity estimation benefits from transsaccadic information integration. *Journal of Vision*, *17*(13), 1–16. https://doi.org/10.1167/17.13.12.doi

CH: Conceptualisation, Methodology, Software, Investigation, Formal analysis, Data curation, Writing - original draft, Visualization. ACS: Conceptualization, Methodology, Supervision, Resources, Writing - review & editing, Funding acquisition.

CH: 75%, ACS: 25%

Study II: Stewart, E. E. M., Hübner, C., & Schütz, A. C. (2020). Stronger saccadic suppression of displacement and blanking effect in children. *Journal of Vision*, *20*(10), 13. https://doi.org/10.1167/jov.20.10.13

EEMS: Conceptualisation, Methodology, Software, Investigation, Formal analysis, Data curation, Writing - original draft, Visualization. CH: Conceptualisation, Methodology, Investigation, Formal analysis, Data curation, Writing - original draft, Visualization. ACS: Conceptualization, Methodology, Supervision, Resources, Writing - review & editing, Funding acquisition.

EEMS: 45%, CH: 40%, ACS: 15%

Study III: Hübner, C., & Schütz, A. C. (2021). A bias in saccadic suppression of shape change. *Vision Research*, *186*, 112–123. https://doi.org/10.1016/j.visres.2021.05.005

CH: Conceptualisation, Methodology, Software, Investigation, Formal analysis, Data curation, Writing - original draft, Visualization. ACS: Conceptualization, Methodology, Supervision, Resources, Writing - review & editing, Funding acquisition.

CH: 75%, ACS: 25%

Study IV: Hübner, C., & Schütz, A. C. (under review). Rapid visual adaptation persists across saccades.

CH: Conceptualisation, Methodology, Software, Investigation, Formal analysis, Data curation, Writing - original draft, Visualization. ACS: Conceptualization, Methodology, Supervision, Resources, Writing - review & editing, Funding acquisition.

CH: 75%, ACS: 25%

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Selbstständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Dissertation selbstständig angefertigt habe. Ich habe mich dabei keiner anderen als der von mir bezeichneten Quellen und Hilfen bedient und alle vollständig oder sinngemäß wiedergegebenen Zitate als solche gekennzeichnet. Ich habe früher noch keine Promotion an der Philipps-Universität Marburg oder an einer anderen Universität eingereicht. Auch die vorliegende Dissertation wurde weder in ihrer jetzigen noch in einer ähnlichen Form bei einer anderen Hochschule eingereicht und hat noch keinen Prüfungszwecken gedient.

Marburg, Juni 2021

Carolin Hübner